THE
AMERICAN NATURALIST

Vol. LXXXV November-December, 1951 No. 825

EFFECTS OF TEMPERATURE AND HOST DENSITY ON THE RATE OF INCREASE OF AN INSECT PARASITE[1]

THOMAS BURNETT[2,3]

Dominion Parasite Laboratory, Belleville, Ontario

Given an unlimited supply of food and a suitable environment, a population of any insect species tends to increase in an exponential manner. In nature, this unlimited growth is prevented by a series of factors that reduce the reproductive rate of the adults and destroy many of the progeny in all stages of their development. A change in the density, that is, the number of individuals per unit volume or area, of the species must result from changes in the intensity of the various mortality factors acting on the species. If these factors are to regulate the density of the insect, they must destroy proportionately more individuals when the density is high than they do when the density is low. These mortality factors include weather, nutrition, intraspecies and interspecies competition, disease, parasites, and predators. By a great oversimplification these factors may be classified into two groups: the physical, and the biotic factors. An extended discussion of these aspects of population ecology, along with extensive bibliographies, may be found in Nicholson and Bailey (1935), Smith (1935), Thompson (1939), and Solomon (1949).

The manner in which a biotic agency exerts its influence in restricting the growth of an insect population is of great practical and theoretical interest. The role that biotic agencies have in population dynamics is well typified by the way in which insect parasites act as mortality factors. The number of hosts destroyed by a parasite and the increase in parasite numbers are closely related to the number of hosts found and attacked. The ability of parasites to contact hosts, or the searching capacity of the parasites, is dependent, among other things, on the density of the hosts. Hence, the mortality caused by insect parasites is controlled, in part, by the density of the host and it is, therefore, said to be a density-dependent factor.

[1]Contribution No. 2868, Division of Entomology, Science Service, Department of Agriculture, Ottawa, Canada.

[2]Entomologist.

[3]The technical assistance of Mr. C. McIntosh is gratefully acknowledged and the writer wishes to thank Professor Thomas Park for reading the manuscript. Thanks are also extended to Mrs. E. C. Pielou for suggesting equations to fit the numerical results.

In addition to destroying individual insects through direct action, physical factors modify the intensity of the action of biotic agencies acting on these insects. Changes in temperature, for example, affect the reproduction of an insect parasite, and the resulting mortality of its host, in two ways. These changes affect the rate at which insect parasites develop and reproduce. They also modify the behavior of the adult female parasites so that their ability to contact hosts when the host density is constant is affected.

The investigation of the mode of action of biotic factors in nature is extremely difficult because of the large number of factors involved and because of the complex inter-relations among them. One approach to this problem is to study one factor, or group of related factors, in the laboratory under simplified conditions. By use of a sedentary form, such as the cocoon of the European pine sawfly, the host species can be maintained at any desired density. The use of chalcid parasites, which are very small, makes it possible to construct a universe, suitable for laboratory investigations, in which the parasite population is unable to find all the hosts that it is potentially capable of parasitizing. In this case, the effect of variations in temperature, host density, and parasite density on the mortality of the host population and on the increase of the parasite population can be examined.

Several species of the sawflies belonging to the family Diprionidae comprise a group of primary importance as defoliators of conifers throughout Canada. *Neodiprion sertifer* (Geoff.), the host used in the present study, is confined to southwestern Ontario, where it is a serious pest of Scotch pine, *Pinus sylvestris* L. As part of the biological control program of the Canada Department of Agriculture against the sawfly pests of conifers, the chalcid parasite *Dahlbominus fuscipennis* (Zett.) has been imported from Europe and hundreds of millions of individuals have been propagated and released in infested areas. It has become established in most of the regions of sawfly infestation.

In this paper, the effects of variations in host density and in temperature on the ability of *D. fuscipennis* to parasitize the cocoon of one of its hosts, *N. sertifer*, are examined. The effect of variations in these two factors on the rate of oviposition of the parasite is also examined.

Ullyett (1936a) investigated the selection by *D. fuscipennis* of hosts (sawfly cocoons) distributed at different densities. He showed (1936b) that the parasite discriminates to some extent between parasitized and unparasitized hosts as well as between true and false hosts. The effect of the density of a host species on the chance of the chalcid parasite *Trichogramma evanescens* Westw. finding its host has been investigated by Flanders (1935) and Laing (1938). Varley (1941) studied the effect of host density on the egg distribution of five chalcid parasites of the knapweed gall fly and (1947) the role of these parasites as density-dependent mortality factors. Ullyett (1947) examined the relationship of mortality factors, including insect parasites, to host density in a study of natural popula-

tions of *Plutella maculipennis* (Curt.). The abilities of three species of predaceous larvae to find their host, the citrus red mite, in a uniform environment, were determined by Fleschner (1950). The effect of variations in the density of a host population on the number of hosts parasitized was analyzed in the laboratory by DeBach and Smith (1941), using puparia of the house fly and the parasites *Nasonia vitripennis* (Walk.) and *Muscidifurax raptor* Gir. and Sand. They found that the higher the host density the greater the number of hosts parasitized by these parasites. However, as the host population was increased the rate of increase in one generation was less than proportional to host density.

MATERIALS AND METHODS

Cocoons of the European pine sawfly *N. sertifer* were used as hosts, and the chalcid *D. fuscipennis* was used as the parasite. The female parasite pierces the cocoon with her ovipositor and lays her eggs on the mature larva inside. Usually, a batch of eggs is deposited during one period of oviposition and about 30 individual parasite larvae can mature on a single host. Most individual females do not attack more than two hosts.

The host cocoons were collected in the field and held in cold storage up to six months before use. To prevent the mature host larvae from destroying the parasite eggs laid on them, the hosts were paralyzed, by dipping them in hot water, before being used. The parasites used in the experiments were reared on *N. sertifer* at a temperature of 22° C. The adult female parasites were held (along with males) with a supply of water for 24–48 hours at this temperature before being used in the experiments.

The experimental universes, one of which is illustrated in figure 1, were thin, square cages of various areas. A sheet of glass, on which was placed a sheet of white blotting paper saturated with water, formed the bottom of the cage. The side, one and one-quarter inches thick, was made of three layers. A rubber gasket rested on the wet blotting paper. Attached to the gasket was a wooden frame in which there were holes, covered with organdy, for ventilation. A thin layer of felt cloth was fastened to the top of the wooden frame. A sheet of glass, resting on the felt on the four sides, formed the top of the cage. The areas of the seven cages used were 16, 25, 50, 100, 200, 300, and 400 square inches.

Each experiment was begun by placing the side of the cage on the wet blotting paper covering the bottom sheet of glass. The bottom of the cage was filled up to the ventilation holes with fresh moss, uniformly dampened by running it through a hand wringer. The upper surface of the moss was smoothed by hand. Twenty-five host cocoons were uniformly distributed, in a 5-by-5 pattern, over the surface of the moss. Twenty adult female parasites were placed near the mid-point of the moss surface but not on a host cocoon. The glass top of the cage was put in position and the cage placed in a dark incubator. The saturation deficiency of the incubator was about 6, but inside the cages it was much lower. At the end of 24 hours, the cocoons were dissected and the number of parasite eggs that each contained was recorded.

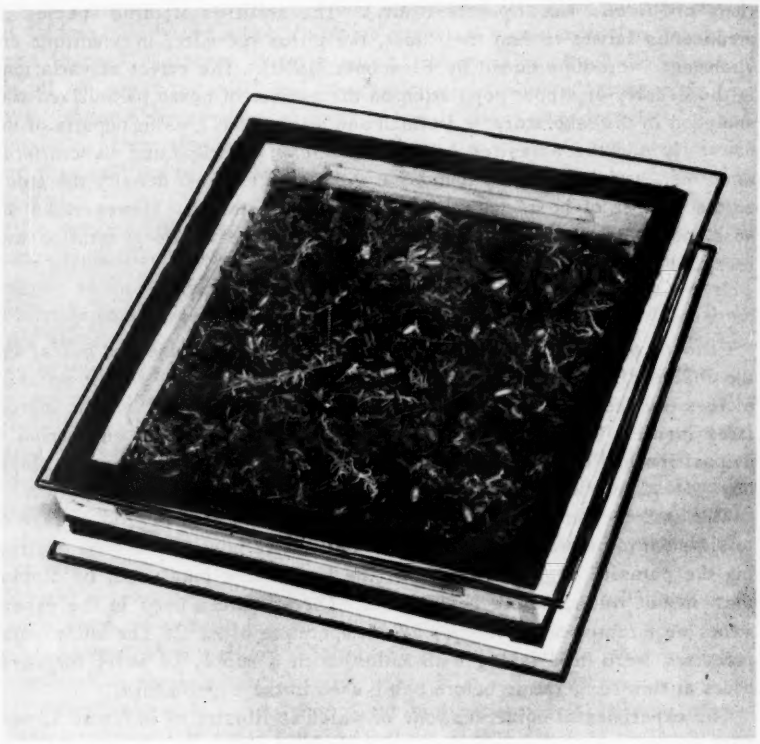


FIGURE 1. Experimental cage used in examination of the effect of host density and temperature on parasitism by *D. fuscipennis*.

Experiments at the seven different densities, that is, 0.06, 0.08, 0.12, 0.25, 0.50, 1.00, and 1.56 cocoons per square inch, were conducted simultaneously to minimize experimental error. Each experiment was replicated 15 times at temperatures of 16, 20, and 24°C.

During the development of the technique used in these investigations a number of variables, in addition to host density and temperature, that affect the number of hosts parasitized and the number of parasite eggs laid became apparent. More hosts were attacked and more eggs were laid: (1) when the adult female parasites were allowed to search for hosts in the light, (2) when the surface of the moss was smooth, (3) when the moss was dry, (4) when the host cocoons were exceptionally large, and (5) when the adult parasites were exceptionally large. Host cocoons completely covered with moss were not attacked.

PARASITISM OF THE HOST

The mean numbers of hosts parasitized by 20 female chalcid parasites when searching at temperatures of 16, 20, and 24°C. for 25 sawfly cocoons,

TABLE 1

NUMBERS OF NEODIPRION SERTIFER PARASITIZED, AT SEVEN HOST DENSITIES AND THREE TEMPERATURES, BY 20 FEMALES OF DAHLBOMINUS FUSCIPENNIS WHEN SEARCHING FOR 25 HOSTS

Host density (cocoons per square inch)	16°C.	20° C.	24°C.
	Mean	Mean	Mean
0.06	1.00 ± 0.195	2.20 ± 0.341	4.00 ± 0.543
0.08	1.33 ± 0.332	4.27 ± 0.573	5.33 ± 0.493
0.12	2.47 ± 0.350	6.47 ± 0.434	7.47 ± 0.486
0.25	3.40 ± 0.542	9.20 ± 0.554	11.20 ± 0.698
0.50	4.60 ± 0.592	12.26 ± 0.650	14.07 ± 0.733
1.00	6.80 ± 0.626	14.33 ± 0.606	16.33 ± 0.843
1.56	7.60 ± 0.616	16.27 ± 0.807	18.20 ± 0.608

uniformly arranged at seven densities, are given in table 1 and shown in figure 2. Table 1 also gives the standard error for each sample of 15 replicates. Table 1 and figure 2 show that with increase in host density the number of hosts attacked by the parasites increased rapidly at the lower host densities but tended to increase more slowly at the higher densities. In no experiment did the 20 parasites attack the 25 hosts. The results

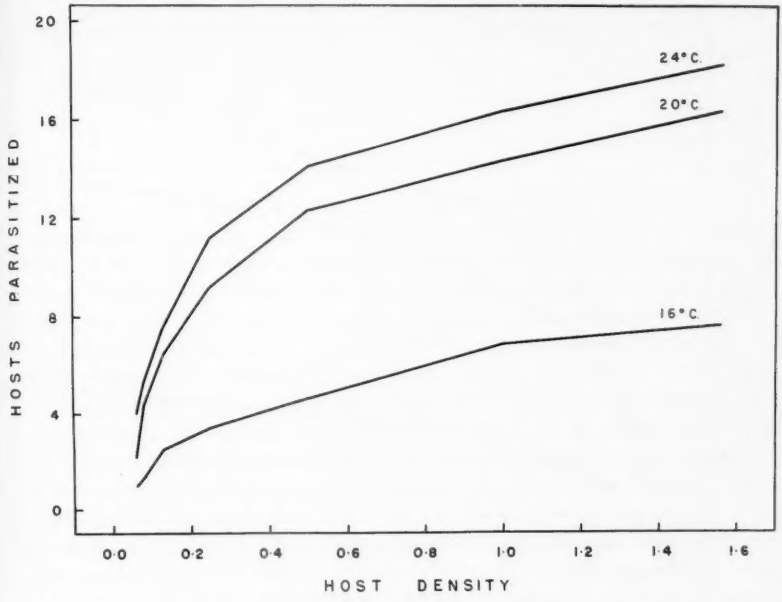


FIGURE 2. The effect of host density (cocoons per square inch) on the numbers of *N. sertifer* parasitized by *D. fuscipennis* at 16, 20, and 24°C.

TABLE 2

NUMBERS OF EGGS LAID, AT SEVEN HOST DENSITIES AND THREE TEMPERATURES, BY 20 FEMALES OF DAHLBOMINUS FUSCIPENNIS WHEN SEARCHING FOR 25 HOSTS

Host density (cocoons per square inch)	16°C.	20°C.	24°C.
	Mean	Mean	Mean
0.06	20.00 ± 4.754	38.47 ± 7.017	88.00 ± 11.385
0.08	25.33 ± 7.131	85.27 ± 13.011	102.87 ± 12.265
0.12	40.80 ± 8.291	118.67 ± 15.224	158.47 ± 13.345
0.25	62.60 ± 9.169	184.00 ± 15.050	243.40 ± 21.410
0.50	98.20 ± 12.874	233.13 ± 16.165	293.93 ± 22.860
1.00	113.07 ± 13.381	287.73 ± 16.102	343.86 ± 22.200
1.56	136.33 ± 14.290	319.86 ± 26.575	402.00 ± 16.490

obtained at 24 and 20°C. were similar to one another except that at 20°C. fewer hosts were attacked. At the highest host density the difference between the numbers of hosts parasitized at these two temperatures was not significant ($P > 0.05$). At 16°C. the number of cocoons attacked was much less, at comparable densities, than the number attacked at 20°C. At the lower densities the increase in the number of hosts parasitized at 16°C. was less rapid than at the higher temperatures. There was considerable variation within each series of replicates. Table 1 indicates that the standard error, in relation to the size of the mean, was much larger when

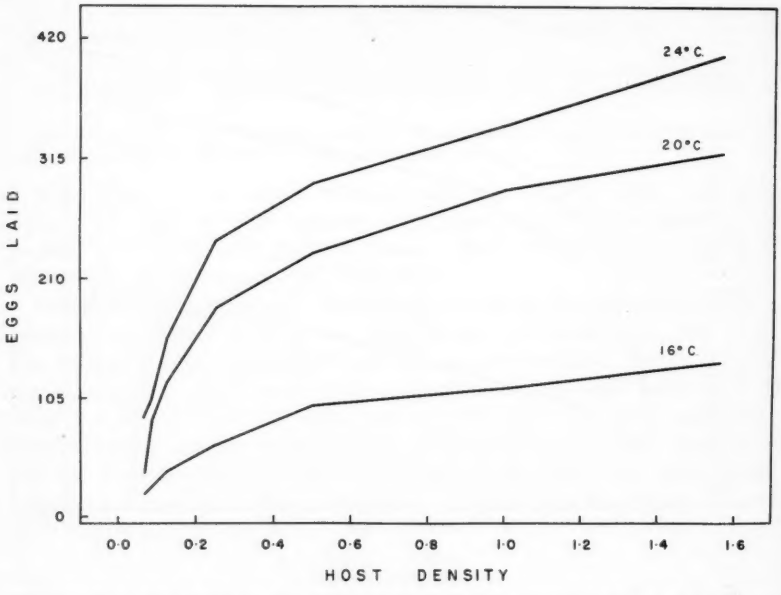


FIGURE 3. The effect of host density (cocoons per square inch) on the numbers of eggs laid by *D. fuscipennis* at 16, 20, and 24°C.

the parasites searched at the lower temperatures for hosts distributed at the lower densities. This was caused by the fact that, at the lower temperatures and densities used, the sample populations of the parasite were approaching the limits of temperature and host density at which they were able to contact hosts.

The average numbers of eggs laid by 20 female parasites at seven host densities and three temperatures are given in table 2 and shown in figure 3. A comparison of figures 2 and 3 shows that the number of eggs laid was relatively the same as the number of cocoons parasitized. At the highest host density the difference between the numbers of eggs laid at 24 and 20° C. was barely significant ($P<0.02$). At the lower temperatures and lower host densities, the variation within each set of 15 replicates was even greater than for the results given in table 1. This increase in variation can be attributed to the great variability usually found in insect oviposition.

TABLE 3

NUMBERS OF EGGS LAID, AT SEVEN HOST DENSITIES AND THREE TEMPERATURES, ON THE HOSTS PARASITIZED BY DAHLBOMINUS FUSCIPENNIS

Host density (cocoons per square inch)	16°C.	20°C.	24°C.
	Mean	Mean	Mean
0.06	21.45 ± 4.382	18.38 ± 2.919	25.07 ± 3.257
0.08	19.67 ± 2.678	19.65 ± 1.454	18.71 ± 1.341
0.12	16.30 ± 1.706	17.97 ± 1.555	20.94 ± 1.258
0.25	20.37 ± 2.744	20.28 ± 1.460	22.03 ± 1.832
0.50	21.67 ± 1.765	19.74 ± 0.957	22.04 ± 1.572
1.00	16.50 ± 1.081	20.74 ± 1.134	20.75 ± 1.016
1.56	17.89 ± 1.060	19.20 ± 1.103	22.02 ± 0.907

In table 3, the average numbers of eggs laid in each parasitized cocoon for the experiments at each density and temperature are given. Although many of the differences between densities at the same temperature and between temperatures at the same density are either not significant or just significant, at 20°C. the mean numbers of eggs per parasitized host tend to be lower than those for 24°C. and at 16°C. the means tend to be equal or lower than at 20°C. As would be expected when fewer cocoons are attacked, the standard error was much larger at the lower densities and temperatures.

In general, the number of cocoons attacked and the number of progeny left by a constant number of parasites increased rapidly with increase of host density, at low densities, but tended to level off with further increase in density. At much higher densities (unrecorded data), however, the values decreased, probably through interference of the females with each other while ovipositing. At a host density of 7.9 cocoons per square inch and a temperature of 24°C. the average number of cocoons parasitized by 20 parasites was 10.9 and the number of eggs laid was 217. At temperatures of 24 and 20° C. the relations of parasite reproduction to host density were

relatively the same, but at 16°C. there was a marked reduction in the numbers of hosts parasitized and the numbers of eggs laid. The numbers of eggs laid on a host at the different densities and temperatures were nearly equal but were slightly reduced as the temperature was lowered. There was a great deal of variation within the replicates, particularly at the lower densities and temperatures.

EFFECT OF VARIATION IN AREA OF UNIVERSE

In the experiments reported in tables 1, 2, and 3 there were two controlled variables: host density and the area of the surface over which the parasites searched for hosts. Possibly the variation in parasitism was related to the area of the universe rather than host density. To eliminate the effect of variation in area, the area of the experimental cages was kept constant at 50 square inches and the number of hosts was varied from 2 to 64, giving the following densities of hosts: 0.04, 0.08, 0.18, 0.32, 0.50, 0.72, 1.00, and 1.28 cocoons per square inch. Twenty adult female parasites searched at 24°C. under conditions otherwise identical with those prevailing in the earlier experiments. The experiments were replicated 15 times.

For the experiments at 24°C., data concerning the number of cocoons parasitized, the numbers of eggs laid, and the numbers of eggs per parasitized cocoon are given in table 4. Figure 4 shows the numbers of cocoons attacked and figure 5 the numbers of eggs laid by the 20 females at the eight different host densities.

TABLE 4

PARASITISM, AT 24° C., OF NEODIPRION SERTIFER BY DAHLBOMINUS FUSCIPENNIS WHEN THE NUMBER OF HOSTS IS VARIED AND THE AREA OF SEARCH IS CONSTANT

Host density (cocoons per square inch)	Cocoons parasitized	No. of eggs laid	No. of eggs per parasitized cocoon
	Mean	Mean	Mean
0.04	1.80 ± 0.144	84.07 ± 28.144	48.53 ± 5.180
0.08	3.13 ± 0.134	143.87 ± 13.565	44.88 ± 3.697
0.18	5.73 ± 0.371	197.00 ± 16.334	35.02 ± 2.572
0.32	9.80 ± 0.470	268.20 ± 18.218	27.23 ± 0.993
0.50	12.93 ± 0.808	296.67 ± 22.228	23.00 ± 1.269
0.72	15.63 ± 0.859	344.93 ± 26.779	22.62 ± 1.214
1.00	17.53 ± 0.833	349.27 ± 17.054	20.14 ± 0.941
1.28	18.40 ± 0.989	361.73 ± 19.521	19.97 ± 0.909

The numbers of cocoons attacked were similar, at comparable densities, to those recorded at 24°C. in table 1. At the lower densities (figure 4) the curve is more nearly linear and this is related to the fact that there was a limited number of cocoons available for attack. The small number of cocoons caused a marked reduction in the standard error.

The average numbers of eggs laid per 20 female parasites were similar, at comparable densities, to those recorded in table 2. There were slightly more eggs laid at the lower densities but about the same number at the higher densities. The variation was much the same.

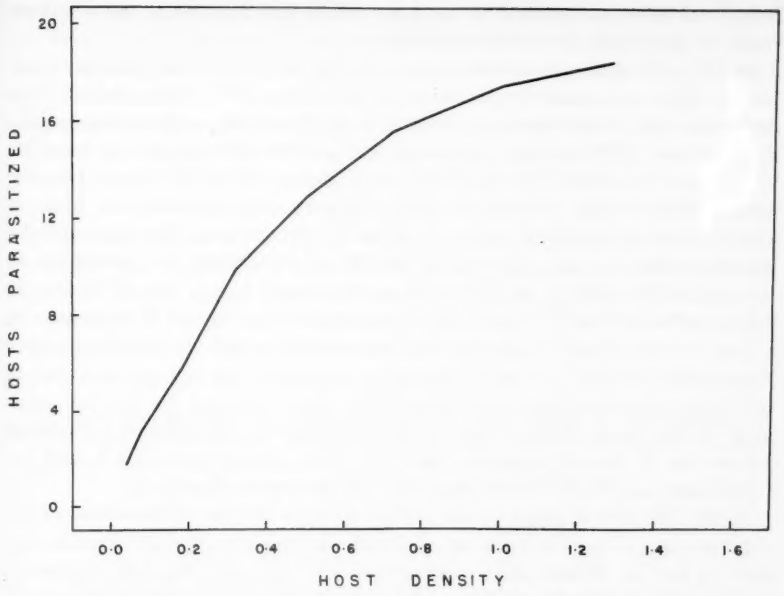


FIGURE 4. The numbers of hosts parasitized at 24°C. when the area of search was constant and the number of hosts varied.

The small number of cocoons used at the lower densities resulted in a large number of eggs being deposited in individual cocoons. This is an indication that there was a considerable amount of superparasitism. The results at the higher densities were similar to those recorded in table 3.

In general, varying the host density by changing the area of search or the number of hosts available did not affect the relationship between the host density and the number of hosts parasitized or the number of eggs laid. Therefore, it appears that the actual, in contrast with the potential, reproductive rate of the parasite varies with the density of the host.

EFFECT OF TEMPERATURE ON OVIPOSITION

The parasites used in the experiments reported in tables 1, 2, and 3 were reared at 22°C. and held after emergence for 24–48 hours at the same temperature. They were then used at temperatures of 16, 20, and 24°C. for a period of 24 hours. Thus, the effect of the variation in temperature in the experimental cages on the oviposition of the parasites was minimized. However, it is possible that the results obtained at the highest density were determined by the effect of temperature on the rate of oviposition of the parasite and not by the effect of temperature on the ability of the parasite to contact the host. To investigate this possibility 100 female parasites were enclosed individually in small glass vials containing two host cocoons. The 100 vials were placed inside an experimental cage, and the cage was placed in an incubator. In this manner, the oviposition of 100

individual females exposed to the same saturation deficiency and temperatures as previously used was recorded.

In table 5 the results of the oviposition by the 100 female parasites are given. With a decrease in temperature from 24 to 16° C. the number of females that failed to oviposit rose from 11 to 25 and the number of eggs laid dropped from 1993 to 1363. However, the number of eggs laid by each female that oviposited decreased by only four. At 16° C. fewer females attacked two hosts. When the parasite attacked two cocoons, one host received more eggs than the other. At 24° C. the cocoons that received the greater number of eggs, in each of the 20 pairs attacked, accounted for 65 per cent of the total eggs laid on those 20 pairs of hosts. At 20° C., for 20 pairs, and at 16° C., for 6 pairs, the percentages were 71 and 76 respectively.

The effect of temperature on the oviposition of the 20 parasites in the experimental cages can be estimated by comparing the results obtained at the highest host-density with one-fifth of those obtained for the 100 parasites in the glass vials. This is done in table 5, in which the observed values for 20 female parasites are taken from tables 1, 2, and 3, and the calculated values are derived from the left-hand part of table 5.

In the first row of table 5, the number of eggs laid by 20 parasites in the experimental cages is seen to approach the number that 20 females are able to lay at 20 and 24° C. but to be only half the possible number at 16° C. In the second row, the numbers of cocoons parasitized in the cages

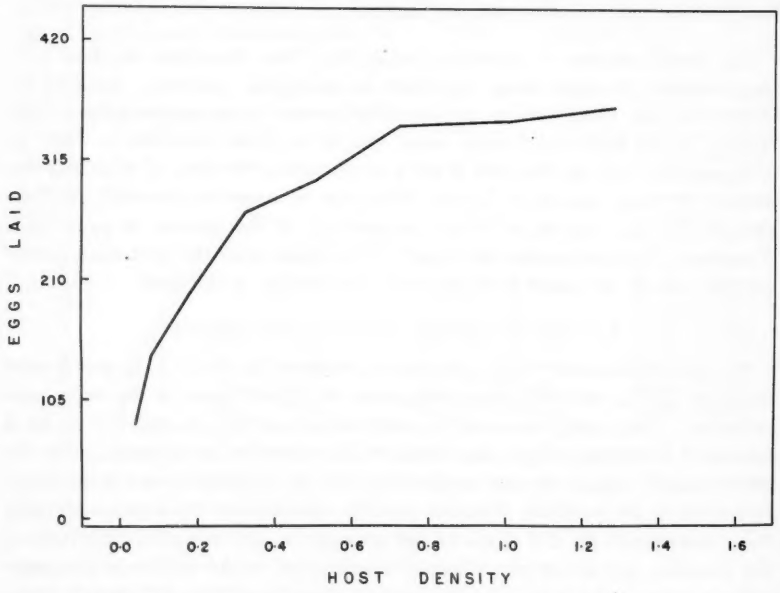


FIGURE 5. The numbers of eggs laid by *D. fuscipennis* at 24° C. when the area of search was constant and the number of hosts varied.

at 20 and 24°C. were equal to the numbers of females that could oviposit but at 16°C. the number was again half that of the potential number. However, at each of the three temperatures the number of eggs laid in each parasitized cocoon was almost identical with the number of eggs that a single female was able to lay in a 24-hour period. Though the number of cocoons parasitized varied from 7 to 18, out of a possible 25, each cocoon parasitized received on the average all the eggs a female was capable of laying. Therefore, although in the glass vials 20 females parasitized an average of 21.8 cocoons (109/5) at 24°C., 21.2 cocoons at 20°C., and 16.2 cocoons at 16°C., in the experimental cages each female probably attacked on the average only one host. In this case, the low fecundity of the parasite at 16°C. was caused by the fact that it parasitized only half of the number that it is capable of parasitizing.

TABLE 5

EFFECT OF TEMPERATURE ON OVIPOSITION OF DAHLBOMINUS FUSCIPENNIS

	100 Females (1 per vial)			20 Females					
				16°C.		20°C.		24°C.	
	16°C.	20°C.	24°C.	Cal.	Obs.	Cal.	Obs.	Cal.	Obs.
Eggs laid	1363	1662	1993	272.60	136.33	332.40	319.86	398.60	402.00
Females ovipositing	75	85	89	15.00		17.00		17.80	
Cocoons parasitized					7.60		16.27		18.20
Eggs per ovipositing female	18.17	19.55	22.39	18.17		19.55		22.39	
Eggs per parasitized cocoon					17.89		19.20		22.02
Females parasitizing one cocoon	69	66	69						
Females parasitizing two cocoons	6	20	20						

In general, at the highest host density, the results obtained at 20 and 24°C. can be attributed to the effect of temperature on the ability of the parasite to lay eggs. Since the curves in figures 1 and 2 are similar in form for the two temperatures, the effect was apparently uniform at the various densities. At 16°C. the results obtained at the highest host density were only half as large as possible. It seems in this case that temperature not only reduced the capacity of the parasite for oviposition but also acted in conjunction with host density to reduce the number of hosts contacted by the parasite.

PARASITIZATION OF THE HOST IN RELATION TO HOST DENSITY

The relation between host density and the increase in a laboratory population of a parasite has been found by Gause (1934) to be curvilinear and to approximate the curve

$$y = a(1 - e^{-kx})$$

where y = number of hosts attacked, x = density of the hosts, a = the limit approached asymptotically by y, e = the base of natural logarithms, and k = a constant related to the rate of change of y. This curve is based on the assumption that the parasite contacts hosts at random. DeBach and Smith (1941) found that this curve approximately described the results obtained, in a single generation, with one insect parasite but not those obtained with a second species. Ullyett (1947) concluded that the host density and parasitism of a natural insect population were related by the function

$$y = ax^b$$

where y = host larvae per host plant, x = parasites per plant, and a and b are constants. Neither of these two formulae gave a sufficiently close approximation to the results observed in this study.

TABLE 6

PARASITIZATION OF THE HOST IN RELATION TO HOST DENSITY

Host density (cocoons per square inch)	Hosts parasitized				Parasite eggs laid			
	16°C.		24°C.		16°C.		24°C.	
	Obs.	Cal.	Obs.	Cal.	Obs.	Cal.	Obs.	Cal.
0.06	1.00	0.72	4.00	4.32	20.00	16.42	88.00	88.28
0.08	1.33	1.37	5.33	5.61	25.33	27.01	102.87	106.45
0.12	2.47	2.29	7.47	7.42	40.80	41.93	158.47	156.15
0.25	3.40	3.83	11.20	10.49	62.60	67.15	243.40	223.24
0.50	4.60	5.29	14.07	13.55	98.20	92.37	293.93	290.34
1.00	6.80	6.56	16.33	16.61	113.07	117.63	343.86	357.53
1.56	7.60	7.19	18.20	18.58	136.33	133.79	402.00	400.52
Chi square		0.2414		0.1057		1.8166		2.5485
d.f.		3		5		6		6
P		> .95		> .99		> .90		> .80

Ullyett (1936a) tested the assumptions that the area searched by individual females of *Dahlbominus fuscipennis* varied inversely as the host density and that the searching was at random. He concluded that climate had no effect on the results obtained.

In the data of this study, it was observed by E. C. Pielou that the rate of change of parasitization of the host varied as the inverse of host density and that consequently the relationship between parasitism and host density might be expressed by

$$y = a + b \ln x$$

where y = no. of hosts attacked, or number of parasite eggs laid, ln x = natural logarithm of host density, and a and b are constants.

TABLE 7

RELATIVE NUMBERS OF HOSTS AND PARASITES EMERGING AT THE END OF A SINGLE GENERATION OF THE PARASITE

Host density (cocoons per square inch)	16°C.			20°C.			24°C.		
	Hosts emerging	Parasites emerging	Ratio parasites/ hosts	Hosts emerging	Parasites emerging	Ratio parasites/ hosts	Hosts emerging	Parasites emerging	Ratio parasites/ hosts
0.06	24.00	20.00	0.8	22.80	38.47	1.7	21.00	88.00	4.2
0.08	23.67	25.33	1.1	20.73	85.27	4.1	19.67	102.87	5.2
0.12	22.53	40.80	1.8	18.53	118.67	6.4	17.53	158.47	9.0
0.25	21.60	62.60	2.9	15.80	184.00	11.6	13.80	243.40	17.6
0.50	20.40	98.20	4.8	12.74	233.13	18.3	10.93	293.93	26.9
1.00	18.20	113.07	6.2	10.67	287.73	26.9	8.67	343.86	39.7
1.56	17.40	136.33	7.8	8.73	319.86	36.6	6.80	402.00	59.1

In table 6, the numbers of hosts parasitized and the numbers of eggs laid at 16 and 24°C. are compared with the numbers expected on the basis that the increase in the rate of parasitization of the host varies with the inverse of host density. In all cases, there is close agreement between observed and calculated values. Table 6 indicates that the effect of host density on the parasitization of the host by *D. fuscipennis* is uniform, in principle, within the normal temperature range of the parasite. The absolute values obtained and the rate at which the effect changes, however, are different at different temperatures.

EMERGENCE OF HOSTS AND PARASITES

Some indication of the effects of temperature and host density on the efficiency of the parasite can be obtained by comparing the relative emergence of the host and that of the parasite adults at the end of a *single generation* of the parasite. In the present case, 20 female parasites were searching for 25 hosts at seven different densities and three different temperatures. It is assumed that all unparasitized hosts emerged as adults, although, of course, this would not occur under natural conditions. Likewise, it is assumed that all parasite eggs developed into adult parasites, for it is known that at least 30 parasite progeny will develop on a single host.

In table 7 the number of hosts, out of the 25 originally exposed to the parasites, that would emerge as adults is compared with the number of parasites that would emerge as adults (taken from table 2) when a parasite generation is taken to be 24 hours. The ratio of parasites to hosts is calculated for each of the three temperatures. As to be expected from table 1, with increase in host density and temperature there was a decline in the number of hosts emerging. The rate of increase of the parasite was less than proportional to the increase in host density, except in the range 0.06 to 0.12 cocoons per square inch, where it was about equal. The ratio of parasites to hosts emerging at the end of a single parasite generation increased with the density of the host and with temperature. At 16 and at 24°C. the increase was as great as tenfold with increase in host density. At 20°C. the increase was greater but the values for the low densities appeared to be a little low. At comparable densities, there was a fourfold increase, between 16 and 20°C., in the ratio of emerging parasites to emerging hosts, while between 16 and 24°C. there was a fivefold increase. In general, the increase of the ratio was approximately proportional to the increase of host density up to 0.25 cocoons per square inch and then it became less.

DISCUSSION

In this laboratory study, the number of hosts destroyed by the parasite *D. fuscipennis* and the increase, in a single generation, of the parasite population were controlled by the two variables: temperature and host density. Any increase in the density of the host caused an increase in the mortality

of the host and brought about an increase in the parasite population. But the rate at which these increases occurred decreased with increments in host density. The operation of this process was greatly influenced by variation in one physical factor, temperature. In the field, this process, though no doubt differing in the magnitude of its effect, provides one check on the unlimited increase of the population of an insect pest. This study indicates that the parasite was least efficient, as a mortality factor, at the lower host densities and temperatures. Since these most nearly approach the conditions found in the field, it seems likely that the parasite attacks far fewer hosts than it is capable of attacking. On the other hand, under these circumstances an increase in host density or temperature produces the greatest response of the parasite as a mortality factor. Through the use of the sedentary host, the sawfly cocoon, and the chalcid parasite *D. fuscipennis*, this aspect of the problem can be examined under simplified field conditions.

SUMMARY

1. The searching of the chalcid parasite *Dahlbominus fuscipennis* (Zett.) for its host *Neodiprion sertifer* (Geoff.) was examined in the laboratory at temperatures of 16, 20, and 24°C. when the host was uniformly distributed at seven densities ranging from 0.06 to 1.56 cocoons per square inch.

2. At lower host densities, the rate of increase of the parasite was rapid, but at the higher host densities it tended to level off.

3. Variations in area of search and in number of hosts available for attack did not account for the variation in parasite increase.

4. At 24 and 20°C. the rate of increase of the parasite, at the highest host density, was controlled by the effect of temperature on the parasite's oviposition but at 16°C. only half as many hosts were attacked and half as many eggs were laid as was possible.

5. In a single parasite generation, the relation between parasitism and host density approximated the curve $y = a + b \ln x$.

6. Increase in temperature and in host density caused a large increase in the ratio of parasites emerging to hosts emerging in a single parasite generation.

LITERATURE CITED

DeBach, P. and H. S. Smith, 1941, The effect of host density on the rate of reproduction of entomophagous parasites. Jour. Econ. Ent. 34:741-745.

Flanders, S. E., 1935, Effect of host density on parasitism. Jour. Econ. Ent. 28:898-900.

Fleschner, C. A., 1950, Studies on searching capacity of the larvae of three predators of the citrus red mite. Hilgardia 20:233-265.

Gause, G. F., 1934, The struggle for existence. Williams and Wilkins, Baltimore.

Laing, J., 1938, Host-finding by insect parasites. II. The chance of *Trichogramma evanescens* finding its hosts. Jour. Exp. Biol. 15: 281-302.

Nicholson, A. J. and V. A. Bailey, 1935, The balance of animal populations. Part I. Proc. Zool. Soc. Lond. 551-598.

Smith, H. S., 1935, The role of biotic factors in the determination of population densities. Jour. Econ. Ent. 28: 873-898.

Solomon, M. E., 1949, The natural control of animal populations. Jour. Anim. Ecol. 18: 1-35.

Thompson, W. R., 1939, Biological control and the theories of the interactions of populations. Parasitology 31: 299-388.

Ullyett, G. C., 1936a, Host density and the success of entomophagous parasites. Nature, London, 137: 742.

1936b, Host selection of *Microplectron fuscipennis* Zett. Proc. Roy. Soc. London (B) 120: 253-291.

1947, Mortality factors in populations of *Plutella maculipennis* Curtis (Tineidae:Lep.), and their relation to the problem of control. Union of South Africa, Dept. Agric. and Forestry, Entomology Memoirs 2: 77-198.

Varley, G. C., 1941, On the search for hosts and the egg distribution of some chalcid parasites of the knapweed gall-fly. Parasitology 33: 47-66.

1947, The natural control of population balance in the knapweed gall-fly (*Urophora jaceana*). Jour. Anim. Ecol. 16: 139-187.

Vol. LXXXV, No. 825 The American Naturalist November-December, 1951

EVIDENCE CONCERNING THE STRUCTURE OF AN EAR OF CORN (ZEA MAYS, L.)[1]

ALLAN B. BURDICK

Iowa State College, Ames, Iowa[2]

The maize ear, with its numerous rows of paired spikelets, is morphologically unique among crop plants. This structure has provoked considerable debate among botanists, geneticists, and morphologists concerning its phylogenetic development, its structure, and its function. The development of the ear has been investigated extensively by Collins (1912, 1919, 1925, 1931), Collins and Kempton (1920), Kempton (1919), Weatherwax (1918, 1919, 1935), Anderson (1944a, 1944b), Bonnett (1940), Mangelsdorf (1945, 1948), Cutler (1946), Fujita (1939), Laubengayer (1948), Stephens (1948), and others. An excellent review has been published by Mangelsdorf (1945) along with convincing evidence that certain characteristics of the ear are explicable on the basis of the Mangelsdorf-Reeves (1939) hypothesis of the origin of corn. He points out that the uniqueness of the maize ear is not due to any one of its morphological characteristics but rather to its combination of being wholly pistillate and having a massive rachis with large, naked caryopses arranged in even numbers of eight or more vertical rows.

A photograph is presented here of two rather unusual ears of corn which serves to show the basic anatomy of the ear. With arguments based on this material I have taken the liberty of speculating about the phylogenetic development of the maize ear.

MATERIALS

The two ears shown in figure 1 came from different hybrid populations. The four-rowed ear developed at the lowermost node of the plant from an F_1 population of Hickory King and a four-rowed sweet variety. The eight-rowed ear appeared in an F_2 population of an eight-rowed yellow starchy line with the four-rowed sweet variety. These two populations were planted in a greenhouse experiment along with others on the 5th of January, 1947, using 2½ inch pots, and later planted to 6-inch pots. A photoperiod of daily decreasing length was provided for the first twenty days and thereafter with the seasonal increasing photoperiod. As the plants began to tassel the tassels were removed as soon as they started shedding pollen. By limiting the amount of pollination the lower ears were induced to develop.

[1]Journal Paper No. J-1965 of the Iowa Agricultural Experiment Station, Ames, Iowa. Project No. 1201.

[2]Now Agronomy Department, University of Arkansas, Fayetteville, Arkansas.

EAR MORPHOLOGY

During the routine examination of about 5,000 immature ears from the greenhouse material, in connection with a study of inheritance of kernel row number, several were found which, from a morphological point of view, were highly interesting. Two of these ears are shown in figure 1.

We may picture, as Collins (1919) and others have done, the phylogenetic development of the maize ear as requiring at least three major steps in addition to the development of the monoecious habit. The progenitor is conceived as being two-ranked, single-flowered, and alternate. These steps, although not necessarily in this chronological order, are the development of the double flowered alicoles, the shortening or compacting of the internode to form the massive rachis and bring the spikelets together in a compact, two-ranked spike, and the elaboration of this two-ranked spike by fusion or twisting to form the many-ranked spike of modern maize.

The elongation at the tip of the four-rowed ear (figure 1), as well as the alternate arrangement of the pairs of kernels in the lower part of the ear, attest to the condensation by "yoking" postulated by Collins (1919). If the elongation evident at the tip were complete, this ear would obviously be an alternate two-ranked spike with double-flowered alicoles.

The basal portion of the eight-rowed ear shows rather well the spiral phyllotaxy, or what has been sometimes called the false spiral phyllotaxy, which may be traced in most normal ears of corn. However, the elongate tip of this ear shows not the spiral phyllotaxy but a whorled one in which the internodes are quite distinct. This may be a small point because the distinction between spiral and whorled phyllotaxy is not always clear, but it does appear reasonable that if the two-ranked spike twisted to produce the four-ranked spike, it would leave a basic spiral type of phyllotaxy, not the whorled one shown here. If, however, each node in the prototype produced two alicoles instead of one, then this, in combination with the "yoking" evident in the four-rowed ear, would be the basis for an eight-rowed ear. This is essentially in agreement with the fusion idea of the elaboration of the two-ranked spike. Corn from the Guarany Indians of Paraguay in crosses with pod corn quite regularly produces these elongate tips showing, definitely, a whorled phyllotaxy (Mangelsdorf, 1945, 1948). Anderson and Brown (1948) have also pointed out that the basic phyllotaxy of the ear and tassel appears to be whorled.

Evidence considered by Stevens (1948) led him to agree, essentially, with Collins' (1919) postulate, namely, that node condensation or telescoping is the basis of the polystichous spike of maize. The evidence presented here cannot be interpreted to differ with this hypothesis. However, the evidence up to now suggests, at least to this writer, that condensation occurred first in a two-ranked spike and was followed by further elaboration at each node.

A word of caution is appropriate in connection with phylogenetic inferences which might be drawn from these ears. If what we observe in North American maize is the result of an undetermined amount of later tripsacoid

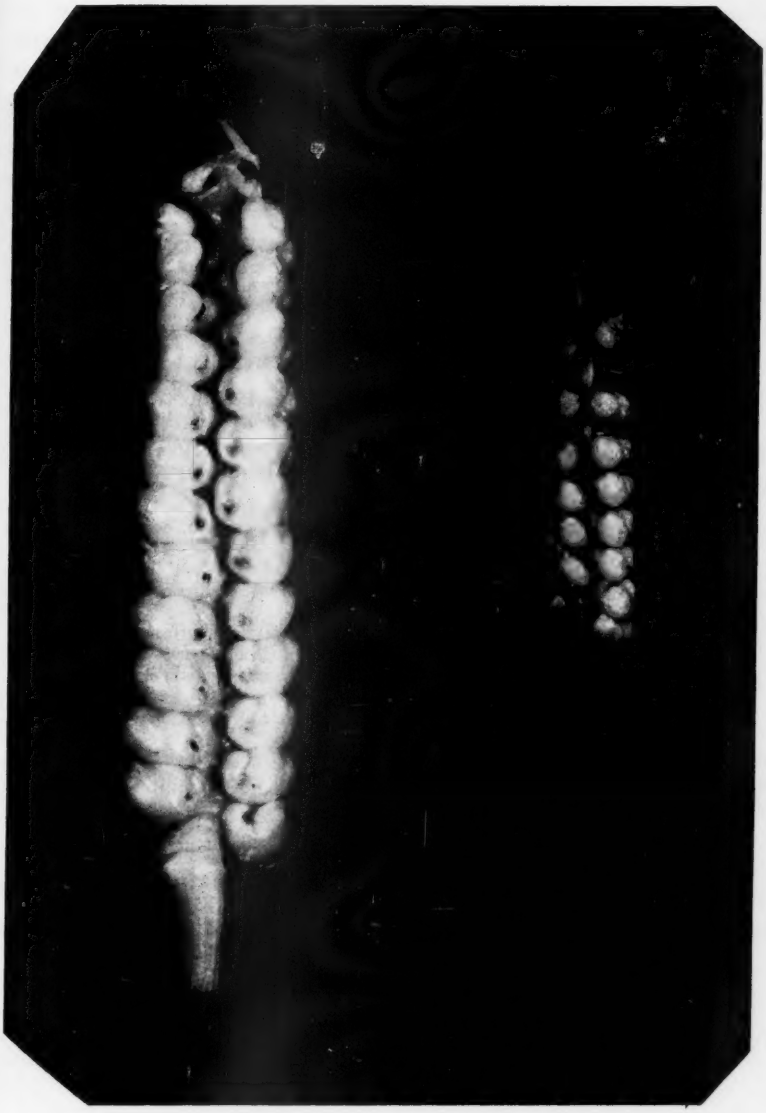


FIGURE 1. Immature four- (left) and eight-rowed (right) ears of corn, showing the pattern of fasciation.

influence, then our conclusions concerning the structure of the ear are somewhat less valid. Considering further that most authorities agree North America is not the most likely point of origin of maize it should follow that evidences from North American maize are drawn from "...a highly derived rather than a primitive condition in Zea maize" (Anderson, 1944). The Guarany material of Mangelsdorf is considered a primitive type; at least it has not suffered the same contamination as has the North American form.

SUMMARY

Evidence is presented which is interpreted as support for the fusion hypothesis of the origin of the maize ear. The basic phyllotaxy of the maize ear appears to be whorled.

LITERATURE CITED

Anderson, Edgar, 1944a, A variety of maize from the Rio Loa. Ann. Mo. Bot. Garden 30: 469–474.

1944b, Homologies of the ear and tassel in *Zea Mays*. Ann. Mo. Bot. Garden 31: 325–342.

Anderson, Edgar, and W. L. Brown, 1948, A morphological analysis of row number in maize. Ann. Mo. Bot. Garden 35: 323–336.

Bonnett, O. T., 1940, Development of the staminate and pistillate inflorescences of sweet corn. J. Agr. Res. 60: 25–37.

Collins, G. N., 1912, Origin of maize. J. Wash. Acad. Sci. 2: 520–530.

1919, Structure of the maize ear as indicated in Zea-Euchlaena hybrids. J. Agr. Res. 17: 127–135.

1925, The "metamorphosis" of Euchlaena into maize. J. Hered. 16: 378–380.

1931, The phylogeny of maize. Bul. Torrey Bot. Club 57: 199–210.

Collins, G. N., and J. H. Kempton, 1920, A teosinte-maize hybrid. J. Agr. Res. 19: 1–37.

Cutler, H. C., 1946, Races of maize in South America. Bot. Mus. Leafl., Harv. Univ. 12: 257–291.

Fujita, T., 1939, Uber die Organstellung bei Maiskolben. Jap. J. Bot. 10: 113–140.

Kempton, J. H., 1919, The ancestry of maize. J. Wash. Acad. Sci. 9: 3–11.

Mangelsdorf, P. C., 1945, The origin and nature of the ear of maize. Bot. Mus. Leafl., Harv. Univ. 12: 33–88.

1948, The role of pod corn in the origin and evolution of maize. Ann. Mo. Bot. Garden 35: 377–406.

Mangelsdorf, P. C., and R. G. Reeves, 1939, The origin of Indian corn and its relatives. Tex. Agr. Exp. Sta. Bul. 574.

Stephens, S. G., 1948, A comparative developmental study of a dwarf mutant in maize and its bearing on the interpretation of tassel and ear structure. Ann. Mo. Bot. Garden 35: 289–299.

Weatherwax, P., 1918, The evolution of maize. Bul. Torrey Bot. Club 45: 309–342.

1919, The ancestry of maize—a reply to criticism. Bul. Torrey Bot. Club 46: 275–278.

1935, The phylogeny of *Zea Mays*. Amer. Midland Nat. 16: 1–71.

Vol. LXXXV, No. 825 The American Naturalist November-December, 1951

THE RANDOM DISTRIBUTION OF GENES ON CHROMOSOMES

MARGARET C. GREEN

The Ohio State University, Columbus 10, Ohio

It is sometimes of interest to know the probable distribution on the chromosomes of a species of the genes affecting a character or characters. As an example, in crosses made for the purpose of combining desirable characteristics of the parent stocks, the ease with which the desired recombinations can be obtained depends, among other things, on the amount of linkage among the genes determining the characteristics. Knowledge of the most probable distribution of the genes concerned gives some idea of the amount of linkage to be expected. As another example, one might wish to know the probability that, of a known number of genes affecting a character, a given number will be located on a single chromosome.

If the chromosomes are approximately equal in size and if the number of genes involved is known or can be estimated, the probabilities for the various possible distributions of the genes on the chromosomes can be calculated by means of the multinomial theorem. The purpose of this paper is to exhibit the way in which this calculation can be accomplished. A general discussion of the multinomial theorem can be found in David (1949).

THE MULTINOMIAL EXPANSION

Let n be the haploid number of chromosomes and let s be the number of genes whose distribution is of interest. If the chromosomes are equal in size and if the distribution of genes on the chromosomes is random, there is equal probability that a given one of the s genes will be located on any one of the n chromosomes. This probability is 1/n. Let p_i (= 1/n) be the probability that a given gene will be located on any one of the chromosomes, where the index i = 1, 2, ..., n. Then the array of probabilities for a given gene is

$$(p_1 + p_2 + \ldots + p_n).$$

The array of probabilities for any other gene is the same as for the first and the array of probabilities for two genes together is the product

$$(p_1 + p_2 + \ldots + p_n)^2.$$

For s genes the array of probabilities can be represented by the expansion of the multinomial to the s power.

Each term in the expansion of the multinomial contains a product of probabilities and a coefficient. In each term there is one p_i element from each of the s quantities $(p_1 + p_2 + \ldots + p_n)$ which are multiplied together in the expansion. Since $p_1 = p_2 = \ldots = p_n = \frac{1}{n}$ this part of the term will be

$p^s = \frac{1}{n^s}$. No particular order of taking the p_i symbols is specified. The coefficient of the term, derived from elementary probability theory, gives the number of different orders in which this particular set of p_i elements can be taken. It is given by the expression

$$\frac{s!}{(1!)^{a_1}(2!)^{a_2}\dots(j!)^{a_j}},$$

where a_i is the number of p_i elements which occur once in the term, that is, the number of chromosomes with one gene, a_2 is the number which occur twice, ..., a_j is the number which occur j times. The complete term of the multinomial expansion is then

$$\frac{s!}{(1!)^{a_1}(2!)^{a_2}\dots(j!)^{a_j}} \cdot \frac{1}{n^s}. \tag{1}$$

To illustrate what this means, consider the problem of the distribution of three genes in an organism with four chromosomes in the haploid set. The chromosomes are numbered from one to four. Let p_1 be the probability that a particular gene is located on chromosome 1, and p_2, p_3, and p_4 the probabilities that it is located on chromosome 2, 3, and 4, respectively. Then $p_1 = p_2 = p_3 = p_4 = \frac{1}{n} = \frac{1}{4}$. The expansion of the multinomial $(p_1 + p_2 + p_3 + p_4)^3$ gives the probabilities for the various possible distributions of the three genes on the four chromosomes. One of the terms in the expansion is $3p_1^2p_2$ (= 3/64) which gives the probability that two genes will be located on chromosome 1 and one on chromosome 2. Without actually expanding the multinomial we could arrive at this probability by use of (1). That is,

$$\frac{3!}{(1!)^1(2!)^1} \cdot \frac{1}{4^3} = \frac{3}{64}.$$

In addition to knowing the value of a single term, we might be interested in knowing the number of similar terms. We might want to know, for example, the number of terms which give probabilities for two genes on any one chromosome and one gene on any other. Such terms would be $3p_1^2p_2$, $3p_1p_2^2$, $3p_3^2p_4$, etc. We want to know how many ways we may make three selections from four chromosomes so that two of them are not taken (have no genes), one is taken once (has one gene), and one is taken twice (has two genes). This is given by the expression

$$\frac{n!}{a_0!a_1!\dots a_j!}, \tag{2}$$

where a_0 is the number of chromosomes with no genes, a_1 the number with 1 gene, ..., a_j the number with j genes. The complete expression which

gives the probability for getting a_0 chromosomes with no genes, a_1 chromosomes with 1 gene, ..., a_j chromosomes with j genes is therefore the product of (1) and (2),

$$\frac{n!}{a_0!\, a_1! \ldots a_j!} \cdot \frac{s!}{(1!)^{a_1} (2!)^{a_2} \ldots (j!)^{a_j}} \cdot \frac{1}{n^s}. \tag{3}$$

In the foregoing example this would be

$$\frac{4!}{2!1!1!} \cdot \frac{3!}{(1!)^1 (2!)^1} \cdot \frac{1}{4^3} = 12 \cdot \frac{3}{64} = \frac{9}{16}.$$

THE NUMBER OF CHROMOSOMES OCCUPIED BY GENES

For small values of s and n it is easy to specify all possible distributions and to calculate the probabilities of their occurrence by the use of (3). For larger values of s and n this may become tedious. If a more limited specification of the distribution is made by combining certain classes of arrangements so that the number of such classes is small, the probabilities can be easily calculated.

Suppose that instead of specifying the number of chromosomes with 0, 1, 2, ..., j genes, we specify only the number with one or more genes. Denote this number by r ($r \leq n$, $r \leq s$). Then n-r is the number with no genes. The probability that all the genes will be located on exactly r of the n chromosomes is the product of the following terms: (a) the number of ways that r chromosomes can be taken out of n chromosomes, (b) the number of ways of arranging s genes on r chromosomes, and (c) the product of probabilities $\frac{1}{n^s}$. The number of ways that r chromosomes can be taken out of n chromosomes is given by the expression

$$n\,(n-1)\,(n-2) \ldots (n-r+1) = \frac{n!}{(n-r)!}.$$

The number of ways of arranging s genes on r chromosomes is the same as the number of ways of dividing s things into r groups. This quantity is given by the expression, $\frac{\Delta^r 0^s}{r!}$, derived by use of the calculus of finite differences (Stevens, 1937). It is tabled as the "differences of zero" (Stevens, 1937) for values of r and s from 1 to 25. The same table may be found in Fisher and Yates (1943) entitled "the leading differences of powers of natural numbers."

The probability that all s genes will be located on exactly r chromosomes is, therefore,

$$\frac{n!}{(n-r)!} \cdot \frac{\Delta^r 0^s}{r!} \cdot \frac{1}{n^s}. \tag{4}$$

TABLE 1

DISTRIBUTION OF s = 15 GENES ON n = 21 CHROMOSOMES. THE PROBABILITIES ARE COMPUTED BY (4) (SEE TEXT).

No. of chromosomes occupied by one or more genes r	$\frac{\Delta^r 0^s}{r!}$	Probability
15	1	0.00104
14	105	0.01562
13	4 550	0.08463
12	106 470	0.22004
11	1 479 478	0.30576
10	12 662 650	0.23791
9	67 128 490	0.10514
8	216 627 840	0.02609
7	408 741 333	0.00352
6	420 693 273	0.00024
5	210 766 920	0.00001
	Total	1.00000

In table 1 for s = 15 genes, n = 21 chromosomes, and for varying values of r are given the values of $\frac{\Delta^r 0^s}{r!}$ and the probabilities calculated from (4) that all genes will be located on exactly r chromosomes. A comparison of the probabilities shows that the most probable arrangement is for the fifteen genes to occupy eleven chromosomes.

A further examination of this example may help to clarify the relationship between (3) and (4). For any value of r it is possible to list the various arrangements which can occur. Thus, in our example, when r = 15 there is only one possible arrangement, one gene on each of fifteen chromosomes (1^{15}). When r = 14 there is also only one arrangement, one gene on each of

TABLE 2

THE WAYS IN WHICH s = 15 GENES CAN BE DISTRIBUTED ON r = 11 CHROMOSOMES. IN THE BODY OF THE TABLE ARE THE NUMBERS OF CHROMOSOMES HAVING THE SPECIFIED NUMBER OF GENES. THE PROBABILITIES ARE COMPUTED BY (3); THE NUMBER OF WAYS THE ARRANGEMENTS CAN OCCUR ARE COMPUTED BY (5) (SEE TEXT).

No. of genes per chromosome					Probability	No. of ways arrangement can occur
1	2	3	4	5		
10				1	0.00062	3 003
9	1		1		0.01552	75 075
9		2			0.01034	50 050
8	2	1			0.13964	675 675
7	4				0.13964	675 675
					0.30576	1 479 478*

*This number equals $\frac{\Delta^r 0^s}{r!}$ for r = 11, s = 15.

thirteen chromosomes and two genes on the remaining chromosome (1^{13}, 2^1). When r = 13 there are two possible arrangements (1^{12}, 3^1; 1^{11}, 2^2), and so on. The five possible arrangements when r = 11 are given in table 2. By use of (3) the probabilities for the occurrence of each can be calculated (next to last column, table 2).

Since $a_0 = (n-r)$, (3) can be rewritten

$$\frac{n!}{(n-r)!} \cdot \frac{s!}{a_1!(1!)^{a_1}a_2!(2!)^{a_2}\dots a_j!(j!)^{a_j}} \cdot \frac{1}{n^s}.$$

By comparison with (4) it can now be seen that

$$\frac{s!}{a_1!(1!)^{a_1}a_2!(2!)^{a_2}\dots a_j(j!)^{a_j}} \tag{5}$$

gives the number of ways in which s genes can occupy exactly r chromosomes when it is specified that a_1 chromosomes shall have 1 gene, a_2 chromosomes shall have 2 genes, ..., a_j chromosomes shall have j genes. $\frac{\Delta^r 0^s}{r!}$ gives the total number of ways in which s genes can occupy exactly r

TABLE 3

ALL ARRANGEMENTS OF s = 10 GENES ON r = 20 CHROMOSOMES IN WHICH THERE ARE 3 OR MORE GENES ON AT LEAST ONE CHROMOSOME. STARRED ARRANGEMENTS ARE THOSE WITH EXACTLY 3 GENES ON ONE CHROMOSOME AND NO MORE THAN 2 GENES ON ANY OTHER.

No. of chromosomes occupied by one or more genes r	No. of genes per chromosome							Probability
	1	2	3	4	5	6		
8	7		1				*	0.05942
7	6			1				0.00801
	5	1	1				*	0.09615
6	5				1			0.00069
	4	1		1				0.00858
	4		2					0.00572
	3	2	1				*	0.03434
5	4					1		0.00004
	3	1			1			0.00046
	3		1	1				0.00076
	2	2		1				0.00172
	2	1	2					0.00229
	1	3	1				*	0.00229
4	all arrangements have 3 or more genes on at least one chromosome							0.00039
3								0.00001
2								0.00000
1								0.00000
	Total							0.22097
	Total of starred arrangements							0.19230

chromosomes or the sum of the values calculated by (5) over all possible arrangements of s genes on exactly r chromosomes. The last column of table 3 gives the calculated number of ways for each arrangement when $s = 15$ and $r = 11$. The sum of these values is $\frac{\Delta^r 0^s}{r!}$

AMOUNT OF LINKAGE

In the example of the distribution of fifteen genes in a species with twenty-one chromosomes (for example, *Triticum vulgare*, in which the chromosomes are nearly equal in size) it can be seen from table 1 that the probability for getting no linkage, that is, for the fifteen genes to occupy fifteen chromosomes, is only 0.00104. It is much more likely that there will be some linkage. The most probable arrangement is that the fifteen genes will occupy only eleven chromosomes, in which case from five to eight genes will be on the same chromosome with at least one other gene. This means that there will most probably be eleven rather than fifteen independently assorting units. The closeness of linkage of those genes which are linked also, of course, affects recombination frequency, but this factor will not be considered here.

NUMBER OF GENES ON ONE CHROMOSOME

Dunn and Caspari (1945) were interested in calculating the probability that, of ten known genes affecting the tail of the mouse, three would be located on the same chromosome. There are twenty pairs of chromosomes in the mouse. They vary somewhat in size, thus failing to fulfill the assumption of equal probabilities ($p_1 = p_2 = \ldots = p_n$) for all the chromosomes. Stevens (1937) has shown that the effect of unequal probabilities is to decrease r, the number of chromosomes which carry genes, and to increase the number of genes per chromosome. The result of the following calculation, based on the assumption of equal probabilities, is therefore an underestimate of the true probability.

The question must be more exactly specified. Of a number of possible questions two are selected for illustration here. (1) What is the probability that there will be three or more genes on at least one chromosome; (2) what is the probability that there will be exactly three genes on one chromosome and no more than two genes on any of the others? The first question includes all possible arrangements having three genes on one chromosome and the answer to it gives the maximum probability for such an arrangement to occur. The second question includes only a small number of arrangements but those which probably are similar to the true arrangement in the mouse.

It is necessary to list all arrangements which meet the specified conditions. This is done in table 3. Fortunately all possible arrangements for $r \leq 4$ are included and the probabilities for the occurrence of these can be calculated from (4). For values of r from five to eight the probabilities

can be calculated from (3). The sum of the probabilities for all arrangements in table 3, 0.22097, gives the probability for getting three or more genes on at least one chromosome. The sum of the probabilities of the starred arrangements, 0.19230, gives the probability for getting exactly three genes on one chromosome and no more than two genes on any other.

I am indebted to Dr. C. A. Lamb for first drawing my attention to this problem. I wish to express my gratitude to Dr. Madge T. Macklin, Mrs. Caroline R. Madison, and Dr. E. L. Green for many helpful discussions and suggestions.

LITERATURE CITED

David, F. N., 1949, Probability theory for statistical methods. pp. 230. Cambridge: Cambridge University Press.

Dunn, L. C., and E. Caspari, 1945, A case of neighboring loci with similar effects. Genetics 30: 543-568.

Fisher, R. A., and F. Yates, 1943, Statistical tables for biological, agricultural and medical research. 2nd ed. pp. 98. London: Oliver and Boyd.

Stevens, W. L., 1937, Significance of grouping. Annals of Eugenics 8: 57-69.

Vol. LXXXV, No. 825 The American Naturalist November-December, 1951

NATURAL SELECTION AND EGG SIZE IN POULTRY

I. MICHAEL LERNER

University of California, Berkeley

It has long been recognized that maximum hatchability in chickens and turkeys is obtained with eggs of intermediate size (Landauer, 1948). The simplest interpretation of this phenomenon is that an absolute physiological optimum size of egg exists for a given set of incubation conditions, higher embryonic mortality being found in eggs that are larger or smaller than this optimum. It now appears that this explanation somewhat oversimplifies the situation, and that the relationship between egg size and hatchability (or more properly reproductive fitness) involves an interaction between artificial and natural selection pressures or the phenomenon designated as genetic homeostasis.

This term suggested by Lerner (1950) refers to the tendency of a population to maintain its genetic composition at an adaptive peak in the face of artificial selection pressures for one or more traits, and seems to be related to what Darlington and Mather (1949) have termed genetic inertia. The self-equilibrating tendency of a population has been demonstrated in a selection experiment with poultry reported by Lerner and Dempster (1951). A line of chickens was subjected to selection for increased shank length. In the early generations genetic gains commensurate with those expected on the basis of an additive gene-action hypothesis were obtained. After a period of such successful selection, progress ceased, in spite of the fact that there was no loss in genetic variability of the character selected for. It was determined that at least one of the reasons for the plateau was traceable to the pressure of natural selection counteracting that of artificial selection. In the plateau period, the fitness (relative number of offspring produced) of extreme deviates (that is, birds with the longest shanks) was below that of the individuals closer to the mean of the population. As a result the population remained at a stationary level, representing an equilibrium between artificial selection for long shanks, and natural selection for fitness.

The situation observed in this instance parallels closely that in the Drosophila selection experiments of Mather and Harrison (1949). The similarity is accentuated by the fact that in the generation following the last one reported by Lerner and Dempster advance in shank length was resumed, suggesting that a new adaptive peak permitting higher levels of this trait is in process of being established by an adjustment of the genetic composition of the population to the conditions imposed on it by the particular selection pressures applied.

One may expect that a balance of forces will operate in a similar manner with respect to any specific quantitative trait, but a precise demonstration

of such a balance may be rather difficult to obtain because of various complicating factors. The case of egg size in birds, it appears upon investigation, offers an opportunity for just such a demonstration. On the basis of the data presented by Lerner and Gunns (1952), auxiliary information from the experimental flock they used in their study, and of an examination of the relevant data in the literature, it can be shown that natural selection does affect egg size in flocks of domestic birds. The direction of this effect is, as expected on the basis of the considerations noted above, counter to the direction of artificial selection, the mean egg size in a population representing the interaction of these two forces.

EXPERIMENTAL EVIDENCE

The experiment conducted by Lerner and Gunns consisted of incubating eggs from a sample of 189 birds, representative with respect to the mean and range of egg weight of a generation of a flock of chickens selected primarily for egg number. The parent flock in the course of its 18-year history has been subjected to mild artificial selection for egg size. Attempts were made to maintain an average spring egg weight in the neighborhood of 56-57 grams. As may be seen from the data given by Lerner and Dempster (1951), the mean egg weights of birds selected as parents in different generations fluctuated about this level. When egg size dropped, the pressure for large eggs was increased; when egg size came up to the desired level, this pressure was relaxed.

In the experiment all birds in the sample were given an equal opportunity to produce chicks in the course of a series of hatches extending from December to June. All eggs laid on 70 days (scattered in this period) by all of the birds concerned were incubated, and records of the actual number of chicks produced by each were taken. Three statistics were thus available for each individual: number of eggs laid, number of chicks hatched, and the percentage of hatchability.

The birds were then grouped according to the characteristic weight of eggs they produced into arrays centering around the mean of the whole population. It was found that the maximum values for all three measurements considered fell into the intermediate egg weight classes. By fitting second degree polynomials to these data, points of maximum fitness (as measured by the three criteria used) with respect to egg weight could be established. All points were found to be below the mean egg weight of the population. It should be noted here that spring-hatched birds in the first laying year (such as were studied here) show increases in their egg size from beginning of lay in the fall to the next spring. In the experiment described it mattered little whether the birds were characterized for egg weight in the fall or in the spring. In either case the optimum egg weight for fitness was below the appropriate mean.

The experiment discussed then shows that the pressure of natural selection in this population is in the negative direction from the mean, artificial selection maintaining average egg weight somewhat above the optimum for

fitness. Hence one might expect that, should the population on which this study was carried out be permitted to reproduce itself without any artificial selection, it would presumably reach an equilibrium mean egg weight, representing an adaptive peak not far removed from the optimum value computed (discrepancies between optima as computed and the equilibria may arise should differential post-hatching mortality exist). No direct evidence of this type is as yet available for the present population, but an approximation of the equilibrium point can be made from the data furnished by Mr. F. T. Shultz, who is presently working with inbred lines derived from the flock under study.

The general outline of this inbreeding study has been given by Lerner (1950). The information pertinent to the present problem comes from the behavior of four lines, in which selection for egg weight was suspended, and of the crosses between them. The lines were isolated from the parent flock in 1945, the 1950 population contemporary with the birds used in the egg weight study representing the sixth inbred generation. At the beginning of the experiment two of the lines were selected for low and two for high November egg production. In the later years because of inbreeding degeneration affecting reproductive fitness the degree of selection practiced was very low if at all existent. Though it is clear that selection for egg number is bound to have some effect on egg size (see, for example, Jull, 1930, on the relation between these two properties), it may be expected that on the average, selection being in both directions, the equilibrium point may be estimated from the means of the lines. The case is strengthened by the addition of information available from reciprocal crosses between the two

TABLE 1

AVERAGE EGG WEIGHTS IN 1950 INBRED LINES AND CROSSES

Line or cross	November		April	
	Number of birds	Mean egg weight	Number of birds	Mean egg weight
Low Number 1	35	47.00	24	55.45
Low Number 2	34	45.88	34	52.91
All low	69	46.45	58	53.96
High Number 1	13	43.31	9	47.51
High Number 2	8	46.50	7	52.27
All high	21	44.52	16	49.59
All inbred lines	90	46.00	74	53.02
Crosses between low number lines	18	48.00	22	55.19
Crosses between high number lines	39	47.64	33	52.68
All Crosses	57	47.75	55	53.68
All birds	147	46.48	129	53.30
Computed optimum: Unweighted		46.29		53.21
Weighted for number of birds in each pen studied		46.30		53.29

low number lines and between the two high number lines. Table 1 shows the mean egg weights of the different lines and crosses.

It may be seen that while some variation between lines exists it is relatively small, particularly for November. It may also be seen from the last three lines of the table that the computed optima are remarkably close to the estimates of equilibrium points. Since the mean egg weights of the birds in the study previously described were higher (48.09 grams for November and 56.39 grams for April), it appears that our interpretation of the phenomenon observed is well supported by this additional evidence.

EVIDENCE FROM THE LITERATURE

Further, confirmation may be sought in the literature on the relation of hatchability to egg size. Since in most flocks of domestic poultry some selection for larger egg size is practiced, it may be expected that the situation described above will prevail in other cases, that is, that the optimum egg weight for reproduction will fall below the mean.

Unfortunately, despite the voluminous data published on the relation between egg weight and hatchability, there are only a few reports which can be used for our analysis, the majority containing material on samples of eggs biassed in different ways. Either the birds from which the eggs were incubated or the eggs themselves were selected in a fashion which would interfere with the determination of the mean and the optimum egg weights.[1] For instance, Hébert and Laugier (1943) set equal numbers of eggs in different weight classes; or as it occurred in one of the sets of data presented by Scott and Warren (1941), the frequency distribution was such that the lowest egg weight class had the largest number of birds, rather than being of the quasi-normal type expected (and usually realized) in unselected samples.

Other reasons for rejection of data for the purposes of our analysis include the presentation of the material in a form combining the results from several years, and even more objectionable from our standpoint, from different seasons. In such instances (for example, Axelsson, 1932) the mean egg weight of the population for a given time of the year is impossible to determine. Still other sets of data in the literature available to us show irregular distributions of hatchability percentages (Benjamin, 1920), so that points of maximum fitness cannot be determined. Finally, others (three of the five sets of Funk, 1934; Warren, 1934; Shibata and Murata, 1936; the second set of Scott and Warren, 1941) show maximum hatchability for the lowest egg weight arrays. It is tempting to speculate that in such cases (all data being from breeding flocks) artificial selection for large egg size was more intense than in the other material under consideration. This,

[1] That selection of birds from which eggs are set can seriously affect the expression of the phenomenon under discussion is illustrated by the fact that Lerner and Dempster (1951) in dealing only with birds selected for breeding from the same flock as studied by Lerner and Gunns (1952) failed to find any obvious relationship between egg weight and fitness.

however, would be an obvious rationalization, and it is more proper to set these data aside as not demonstrating the more commonly observed curvilinear relation between hatchability and egg weight.

All the other sets of data located have been analyzed for mean weights and points of maximum hatchability. It should be noted that the analysis of these can be considered to be valid only as an approximation: (1) the

TABLE 2

RELATION BETWEEN OBSERVED MEAN EGG WEIGHT AND COMPUTED EGG WEIGHT, OPTIMUM FOR HIGH HATCHABILITY

Set no.	Population studied	All eggs set		Fertile eggs set		Reference ‡
		Mean egg wt.	Optimum egg wt.	Mean egg wt.	Optimum egg wt.	
1.	W. Leghorn pullets	55.34	53.66			Dunn, 1922
2.	" " "			55.41	53.04	" "
3.	W. Leghorn hens	57.77	52.33			" "
4.	" " "			57.69	48.69	" "
5.	Chickens, breed not specified	56.11	57.54			Halbersleben and Mussehl, 1922
6.	Chickens, breed not specified			56.01	54.85	Halbersleben and Mussehl, 1922
7.	B. P. Rock pullets	55.46	54.44			Jull and Haynes, 1925
8.	" " " "			55.47	52.79	Jull and Haynes, 1925
9.*	R. I. Red pullets			59.65	57.77	Funk, 1934
10.*	R. I. Red hens			60.85	55.95	Funk, 1934
11.	Turkeys, mixed breeds			77.33	79.94	Byerly and Marsden, 1938
12.	Turkeys, breed not specified			88.26	63.14	Insko, MacLaury and Baute, 1943
13.	Turkeys, breed not specified			89.62	79.39	Insko, MacLaury and Baute, 1943
14.	Turkeys, breed not specified			86.87	89.28	Insko, MacLaury and Baute, 1943
15.	Turkeys, breed not specified			89.00	77.80	Insko, MacLaury and Baute, 1943
16.	Turkeys, breed not specified			87.63	83.20	Insko, MacLaury and Baute, 1943
17.*	Leghorn pullets (November)	48.64	47.44			Lerner and Gunns, 1952
18.*	Leghorn pullets (April)	57.03	51.93			Lerner and Gunns, 1952
19.*†	Leghorn pullets (November)	48.64	46.30			Lerner and Gunns, 1952
20.*†	Leghorn pullets (April)	57.03	53.29			Lerner and Gunns, 1952

* Bird averages rather than individual eggs.

† Based on number of chicks produced rather than on percentage hatch.

‡ Addendum: The paper by Skoglund, Tomhave and Mumford (1948, Poultry Sci. 27: 709-712) was inadvertently overlooked when Table 2 was being compiled. Their extensive data appear to substantiate the thesis advanced here, particularly in the demonstration of concurrent increases in the mean and optimum egg weights with advancing age of the birds.

means computed are for populations of eggs set, and not for the parental flocks; (2) information on the type of sampling is generally lacking; (3) data on hatchability only, rather than on reproductive fitness are available.

Nevertheless, as it may be seen from table 2 in all but three sets of data (appearing in italics) the optimum egg weight as computed under the direction of Dorothy C. Lowry in the same manner as for the data of Lerner and Gunns, falls below the mean. No immediate explanation for the departure from expectation of two of these (5 and 14) is available. The third one (11), as it happens, provides a striking confirmation of the thesis advanced, since it is derived from a turkey flock, in which selection has been practiced for small body size, and hence for small egg size. In such a situation the prediction from our hypothesis is that the optimum will be higher than the mean, as is clearly the case. Thus in 18 out of 20 available examples (not all of which are, of course, independent of each other) the expectation is fulfilled.

There seems to be little doubt that natural selection is a force of appreciable magnitude in the determination of the average egg size exhibited by domestic populations of birds. The differential reproductive fitness of birds with different genotypes for egg size may be due to a reduction from the potential number of offspring in any one of the stages where losses can occur. Thus the number of eggs produced by each dam, their fertility and their hatchability may all be involved in this process. It is quite likely that in different cases one or more of these operate. Thus in the experiment of Lerner and Gunns (1952) both egg production and the hatchability of all eggs set showed a curvilinear relation to egg weight. In the material of Kumanov (1948), which was not included in our table 2 because of the uncertainty regarding the nature of the data (it appears as if pooling of seasons and years, such as made by Axelsson, 1932, was also resorted to here), there is a suggestion that fertility may be implicated, as it may be seen from the following figures:

	Mean egg weight	Optimum egg weight	
All eggs	56.24	52.41	(based on fertility)
		57.78	(based on hatchability)
Fertile eggs	56.14	54.01	(based on hatchability)

On the other hand, the data of Düzgüneş (1950) on the reproductive fitness of inbred lines indicate that the hatchability of fertile eggs may be the major contributor to variance in fitness. The precise physiological mechanism involved in any given instance of genetic homeostasis is thus a subject for future investigation.

Similarly, the particular genetic mechanisms underlying the balance between natural and artificial selection which determines the observed average egg size in each case need thorough study. Simple pleiotropy or linkage are possible; but overdominance, epistasis, and balanced heterozygosity of chromosome segments or whole chromosomes may also be involved. Examples for most of these mechanisms can be adduced in different situations (Caspari, 1951; Nybom, 1950; Mather and Harrison, 1949; Dobzhansky,

1947). Which ones are specifically applicable to the situation at hand cannot be said at this time. It is clear, however, that in animal breeding practice, the phenomenon of genetic homeostasis must be taken into account in the formulation of efficient breeding systems.

SUMMARY

Experimental evidence is given for the operation of natural selection for egg size in populations of domestic fowl. As a rule the counter-force of artificial selection in commercial flocks maintains average egg size above the optimum for reproduction.

LITERATURE CITED

Axelsson, J., 1932, Variation and heredity of some characters in White Leghorns, Rhode Island Reds and Barnevelders. I. Lund Univ. Arsskr., N. F. 2, 28, (4), 196 pp.

Benjamin, E. W., 1920, A study of selections for the size, shape and color of hen's eggs. Cornell Agr. Exp. Sta. Mem. 31:191-312.

Byerly, T. C., and S. J. Marsden, 1938, Weight and hatchability of turkey eggs. Poultry Sci. 17:298-300.

Caspari, E., 1951, On the biological basis of adaptedness. Amer. Scientist, 39:441-451.

Darlington, C., and K. Mather, 1949, The elements of genetics. 446 pp. Allen and Unwin, London.

Dobzhansky, Th., 1947, Adaptive changes induced by natural selection in wild populations in *Drosophila*. Evolution 1:1-16.

Dunn, L. C., 1922, The relationship between the weight and the hatching quality of eggs. Storrs Agr. Exp. Sta. Bull. 109:93-114.

Düzgüneş, O., 1950, The effect of inbreeding on reproductive fitness of S.C.W. Leghorns. Poultry Sci., 29:227-235.

Funk, E. M., 1934, Factors influencing hatchability in the domestic fowl. Mo. Agr. Exp. Sta. Bull. 341, 22 pp.

Halbersleben, D. L., and F. E. Mussehl, 1922, Relation of egg weight to chick weight at hatching. Poultry Sci. 1:143-144.

Hébert, J., and H. Laugier, 1943, Probabilité d'éclosion des oeufs en fonction de leur poids. Rev. Can. Biol., 2:113-119.

Insko, W. M., Jr., D. W. MacLaury, and E. A. Baute, 1943, Weight of turkey eggs in relation to hatchability. Ky. Agr. Exp. Sta. Bull. 449, 16 pp.

Jull, M. A., 1930, Problems in egg weighing in relation to production. Poultry Sci. 9:207-218.

Jull, M. A., and S. Haynes, 1925, Shape and weight of eggs in relation to their hatching quality. J. Agr. Res. 31:685-694.

Kumanov, S., 1948, The influence of some factors upon the fertility and hatchability of hens' eggs. 8th World's Poultry Congr., Off. Rpt. 1:320-325.

Landauer, W., 1948, The hatchability of chicken eggs as influenced by environment and heredity. Storrs Agr. Exp. Sta. Bull. 262, 231 pp.

Lerner, I. M., 1950, Population genetics and animal improvement. XVIII - 342 pp. Cambridge University Press.

Lerner, I. M., and E. R. Dempster, 1951. Attenuation of genetic progress under continued selection in poultry. Heredity 5:75-94.

Lerner, I. M., and C. A. Gunns, 1952, Egg size and reproductive fitness. In press.

Mather, K., and B. J. Harrison, 1949, The manifold effect of selection. Heredity 3:1-52, 131-162.

Nybom, N., 1950, Studies on mutations in barley. I. Superdominant factors for internode length. Hereditas 36:320-328.

Scott, H. M., and D. C. Warren, 1941, The relation of total weight and the weight of component parts of the egg to hatching power. Poultry Sci. 20:75-78.

Shibata, S., and A. Murata, 1936, Studies on the hatching of the hen's egg. Imp. Zootechn. Exp. Sta. Chiba-Shi, Spec. Bull. 13, 27 pp. (in Japanese).
Warren, D. C., 1934, The influence of some factors on the hatchability of the hen's egg. Kans. Agr. Exp. Sta. Bull. 37, 42 pp.

Vol. LXXXV, No. 825 The American Naturalist November-December, 1951

SPERMATOGENESIS OF THE HORNED LIZARD PHRYNOSOMA CORNUTUM[1]

L. F. CAVAZOS

Iowa State College

INTRODUCTION

One of the important cytological aspects of vertebrate phylogeny deals with the investigation of the mutual connections between the chromosomes of reptiles and those of birds and mammals. Results obtained from the study of birds have shown the male homozygous and the female heterozygous for sex, whereas in mammals the opposite condition prevails. The biological basis for this difference is not known, but it is possible that a systematic investigation of reptilian chromosomes may yield information of value in explaining this situation. Investigators in several parts of the world have worked on this problem and among them are: Matthey (1949) in France; Nakamura (1935), Makino (1949), (1951), and Momma (1949) in Japan; as well as the earlier work of Painter (1921) in this country. Results from chromosome studies on 85 species of reptiles have been reported according to Makino and Momma (1949). In most of these studies, the emphasis has been placed upon the determination of the diploid number of chromosomes as observed in the spermatogonia.

The purpose of this investigation is to follow the chromosomes through spermatogenesis of a reptile, the horned lizard, *Phrynosoma cornutum* (Harlan).

MATERIALS AND METHODS

The specimens used in this study were collected during their breeding season from May through August, 1950, in the vicinity of Lubbock and Kingsville, Texas. The animals were killed by decapitation following the recommendation of Painter (1934) who has suggested the use of anaesthetics tends to affect the chromosomes. The testes were removed, placed in fixing fluid, and the tubules teased apart to facilitate penetration by the fixative.

Three methods of fixation were used in this investigation. These included: (1) Bouin's (1936), modified by increasing the acetic acid content from 5 to 20 cc.; (2) Painter's modification of Bouin-Allen's fluid (1934); and (3) an unpublished fixative developed by Cross (1950) consisting of 60 cc saturated picric acid solution, 25 cc of 37 percent formaldehyde, and 25 cc glacial acetic acid. Prior to using, 1.5 grams of picric acid and 3

[1] A thesis submitted to the Graduate Faculty of Texas Technological College in partial fulfillment of the requirements for the degree of Master of Arts. The study was under the direction of Dr. J. C. Cross.

grams of urea were added. Following fixation the tissues were dehydrated in the usual series of alcohols, cleared in xylol, and embedded in paraffin.

The increase in the acetic acid content of Bouin's fluid facilitated the spreading of the chromatin material so that the morphological elements of the nucleus could more easily be examined in detail. This method was also an improvement in fixation of primary and secondary spermatocytes. However, the spermatogonia fixed in this manner were not suitable for counting the chromosomes of the diploid complex, but the prophase stages were satisfactory. Painter's modification of Bouin-Allen's (1934) was found to be unsatisfactory in this work. However Painter (1921), working on the spermatogenesis of reptiles, used this method of fixation with excellent results.

In this investigation the fixative developed by Cross (1950) was the most successful of those tried because excellent conditions were obtained for the study of spermatogonia. The chromosomes were well spread with a minimum amount of overlapping and could be counted in most of the complexes. The prophase stages, as well as the primary and secondary spermatocytes, were also good for this purpose.

The staining technique was a 3 percent ferric ammonium sulfate mordant followed by four hours in 0.5 percent hematoxylin. Destaining was carried out in 1.5 percent ferric ammonium sulfate followed by ten minutes in saturated picric acid. The picric acid dissolved some of the cytoplasmic inclusions and permitted critical observation of the chromosomes. No counterstaining was employed in this study.

RESULTS

Spermatogonia. Dividing spermatogonia (figs. 1 and 2), when seen from the equatorial plate, polar view, showed an outer circle of large metacentric or V-shaped chromosomes surrounding the dot-like ones which were located in the center of the cell. Throughout this study the V-shaped elements are referred to as macro-chromosomes whereas the dot-like ones are termed micro-chromosomes. Twelve macro-chromosomes and 24 micro-chromosomes were found in the spermatogonia of *Phrynosoma cornutum.* Therefore, the diploid number is 36. The shape of the macro-chromosomes was so distinctive that it was not difficult to pair the homologous mates, as shown in fig. 3. However, no attempt was made to pair the micro-chromosomes due to their small size and irregular appearance. No chromosomal satellites were observed, and the staining technique obscured the centromere as well as the nucleolar organizer.

In general, most of the small chromosomes were well distributed and centrally located within the metaphase plate, but some were very close to the peripherally located larger elements, therefore making their enumeration difficult. Twenty-four micro-chromosomes are seen in both of the spermatogonia shown in figs. 1 and 2. This number corresponds with the 12 micro-chromosomes found in the primary spermatocyte.

Primary Spermatocyte. The leptotene stage of the prophase, as illustrated in fig. 4, presented a fine network of chromatin material with very

PLATE I

2

3

4

5

6

7

8

9

long and slender filaments. At this stage the chromomeres were visible as small beads extending the entire length of the chromosomes. Two large nucleoli are shown in fig. 4, and there was no evidence of the micro-chromosomes at this stage. No zygotene stages were found.

The amphitene stages of the prophase, as shown in fig. 5, were very numerous. In general, the chromosomes exhibited a lack of uniformity, and as a result the cell had a rough appearance. The nucleoli, which were visible in the leptotene cells, were not observed in succeeding stages.

In the early pachytene, as illustrated in fig. 6, the chromosomes became shorter and had a rather coarse appearance, but this was possibly due to the contraction of the chromatin matter. No polarization of the chromosomes was visible in any of the observed earlier stages.

Diakinesis, as shown in fig. 7, exhibited six large tetrads and was characterized by a constriction of the filaments to such a degree that they became large broad bands of chromatin. This constriction was to a much greater degree than that found in any of the earlier prophase stages. The stippled areas, as indicated in fig. 7, represent the regions in which granulated chromatin material was visible.

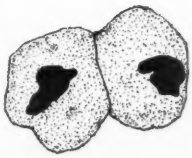
The polar view of the primary spermatocyte, illustrated in fig. 8, indicated that the haploid number of chromosomes was 18. This stage contained 6 macro-chromosomes and 12 micro-chromosomes. The latter elements were difficult to locate, as there was always the possibility that some of them might be obscured by the macro-chromosomes.

Many of the primary spermatocytes showed the tetrads in the metaphase side-view. There were 6 of the larger chromosomes present, most of them being hat-shaped; but due to their large size there was a great deal of overlapping. In general, the micro-chromosomes were not visible in most of the side views of the metaphase plates of the primary spermatocytes. In a few cells one or two of the micro-chromosomes were observed. However, in the majority studied, they were covered by the larger tetrads.

In fig. 9 a primary spermatocyte is represented in the anaphase stage as its chromosomes are grouping to form the secondary spermatocyte. This figure shows both sets of dyads as they were migrating towards their respective poles. The secondary spermatocytes had six large chromosomes. It was not possible to make an accurate count of the micro-chromosomes of the secondary spermatocytes.

Metamorphosis of Sperm. The metamorphosis of the sperm of *Phrynosoma cornutum* could be easily traced by the staining method used in this investigation. After the chromosomes had reached their respective poles at the conclusion of telophase II, they lost their identity and massed together. Following this, the cells separated, forming the two spermatids as shown in fig. 10. At this stage of development a general grouping of the chromatin material took place and a small sphere was formed within the cell membrane as illustrated in fig. 11. Elongation of the nucleus took place at this time and continued until this structure assumed a rod-shaped appearance and was located in the center of the cell as shown in figs. 12 and 13. At this

PLATE II



10

11

12

13

14

15

16

time the chromatin began to migrate towards the edge of the cell membrane and soon was free of the cytosome (figs. 14 and 15). After this stage, the whip-like flagellum was formed. With the staining methods employed in this study, it was not possible to trace the formation of the acrosome, neck, or middle piece.

DISCUSSION

The spermatogenesis of *Phrynosoma cornutum* is typical of those previously described for the family Iguanidae (Painter, 1921), but two important differences exist: (1) the formation of sex chromosomes and (2) the absence of giant spermatozoa. Painter (1921) published plates illustrating the passage of the undivided X-chromosome to one pole of the first division spindle in animals representing the genera *Anolis* and *Sceloperus*. However, this early migration of one chromosome to the pole was not observed in this study of *P. cornutum*.

It was not possible to accurately distinguish the sex chromosomes from the autosomes in this species. Due to the pairing of the macro-chromosomes, the X-Y condition was not apparent in these elements. This difference may be genetic, but the morphology of the chromosomes offered no explanation. However, Nakamura (1935), working near Kyoto, Japan, found evidence for sex chromosomes in male lizards belonging to the genus *Takydromus*. The spermatogonia in the three species studied revealed 38 chromosomes. Thirty-six of these were of various sizes and therefore this investigator was unable to sort them into categories of macro- and micro-chromosomes. He concluded that the other two chromosomes were the sex chromosomes representing the X-X condition. It is possible that the X-X or X-Y arrangement may exist in the micro-chromosomes of the horned lizard, but due to their small size, it was not possible to pair these elements. If sex is determined by the macro-chromosomes, then due to their perfect pairing the X-X condition would likely prevail in *P. cornutum*.

The horned lizard, which belongs to one of the families studied by Painter (1921), fits into the typical chromosomal pattern of reptiles as described by him. He pointed out that the chromosomes of lizards show a sharp division into size groups of macro- and micro-chromosomes. In all the lizards examined, 12 V- or U-shaped macro-chromosomes were present, but variation existed in the numbers of the smaller elements.

SUMMARY

A study has been made of the spermatogenesis of the Texas horned lizard, *Phrynosoma cornutum* (Harlan). Dividing spermatogonia showed 36 chromosomes; 12 of these were V-shaped macro-chromosomes and 24 were dot-like micro-chromosomes. In the primary spermatocytes there were six macro-chromosomes and twelve micro-chromosomes. Some of these stages, when seen in metaphase side view, had six hat-like tetrads. In polar view, the secondary spermatocyte presented six large chromosomes arranged in a circle surrounding the micro-chromosomes. The metamorphosis of sperm is

described. No evidence was found to suggest the presence of sex chromosomes in this species. However, the X-X condition may exist in the macrochromosomes.

LITERATURE CITED

Cross, J. C., 1950, Personal communication.

Guyer, M. F., 1936, Animal micrology. pp. 9. Univ. of Chicago Press. Fourth Ed.

Makino, S., 1951, An atlas of the chromosome numbers in animals. pp. 242-249. The Iowa State College Press. Second Ed.

Makino, S., and E. Momma, 1949, An idiogram study of the chromosomes in some species of reptiles. Cytologia 15:96-108.

Matthey, R., 1949, Les chromosomes des vertebres. pp. 186-196. F. Rouge-Lausanne.

Nakamura, K., 1935, Studies on reptilian chromosomes. IV. Chromosomes of Takydromus spp. (lizards). Memoirs College of Science, Kyoto Imperial Univ. Series B, 10:341-353.

Painter, T. S., 1921, Studies in reptilian spermatogenesis. 1. The spermatogenesis of lizards. J. Exp. Zool. 34:281-318.

1934, A technique for the study of mammalian chromosomes. Anat. Rec. 27:77-86.

EXPLANATION OF FIGURES

All the drawings were made with the aid of an Abbe camera lucida and at a magnification of X3000.

Plate I.

FIGURES 1 and 2. Dividing spermatogonia of *Phrynosoma cornutum*, as seen from the equatorial plate, polar view, showing thirty-six chromosomes.

FIGURE 3. Serial alignment of macro-chromosomes of fig. 1.

FIGURE 4. Leptotene stage showing a fine network of chromatin.

FIGURE 5. Amphitene stage.

FIGURE 6. Pachytene stage.

FIGURE 7. Diakinesis stage.

FIGURE 8. Polar view of the primary spermatocyte showing eighteen chromosomes.

FIGURE 9. Anaphase stage of the primary spermatocyte as its chromosomes are grouping to form the secondary spermatocyte.

Plate II.

FIGURE 10. Spermatids.

FIGURE 11. A single spermatid.

FIGURE 12. Elongation of the chromatin material.

FIGURE 13. Migration of chromatin towards the edge of the cell membrane.

FIGURES 14 and 15. Chromatin free from the cytosome.

FIGURE 16. Spermatozoon.

Vol. LXXXV, No. 825 The American Naturalist November-December, 1951

THE FATE OF YEAST IN THE DIGESTIVE TRACT OF DROSOPHILA

A. M. EL-TABEY AWAB SHIHATA[1] AND E. M. MRAK[2]

University of California, Berkeley, California

The importance of yeasts as a food for Drosophila was well established by Delcourt and Guyenot (1910), Guyenot (1913), and Northrop (1916 and 1917). In line with this, it has been customary for many years for biologists, and particularly geneticists, experimenting with Drosophila to use yeast in the food of their fly cultures. Considerable information on the nutritive value of yeasts to Drosophila is available in reports by Baumberger (1919), Chevais (1942), Chiang and Hodson (1950), Gordon and Sang (1941), Robertson and Sang (1944), and others. There is, however, no information on the fate of yeasts ingested by Drosophila or the rate at which they are digested. Recently the authors were concerned with the isolation of yeasts from the intestinal tracts of Drosophila flies collected in the mountains of central and southern California. The flies were shipped to Berkeley and yeast isolation made in the shortest time possible after collection. The initial collections of flies yielded relatively few yeasts. Since the crops of the flies were well distended at the time of collection, it was presumed that the yeasts were digested before isolations were attempted in the laboratory. It became necessary to develop a procedure for the transportation of flies to the laboratory with a minimum destruction of yeast, or abandon the project. In the development of this procedure, certain data of interest to Drosophila workers were obtained. These are reported below:

DIGESTION OF YEAST CELLS BY DROSOPHILA

D. pseudoobscura flies were held in a bottle at room temperature without food for twenty-four hours before the introduction of a paste of bakers' yeast on a glass slide. The flies were permitted to feed on the yeast paste for two hours, after which time they were well fed, as indicated by distention of the entire abdomen. The flies were then removed and placed in clean bottles which were stored at different temperatures. At various intervals, flies were withdrawn from each bottle and the alimentary tract removed from plating. The number of yeast cells in the alimentary canal of each fly was determined by the quantitative plating method as described by Henrici and Ordal (1948). The results of these tests are given in table 1.

It is obvious that digestion is very rapid at room temperature and much slower when the temperature is appreciably lower. The crops of flies held

[1] Now at Farouk I University, Alexandria, Egypt.
[2] Now at the University of California, Davis, California.

at room temperature were almost empty 24 hours after feeding. This is in agreement with the findings of Dobzhansky and Epling (1944) that contents of the crop pass into the gut in about 24 hours after ingestion of the food. On the other hand, crops of flies stored at 0°C. appeared full at the time of dissection, but the extent of distention decreased when the storage period was increased. The experiment showed the importance of cooling flies as soon as they are collected, so the internal flora can be studied without much change during transportation. Accordingly the writers adopted the following procedure for the handling and transportation of flies from their native habitat to the laboratory.

TABLE I

SURVIVAL OF YEASTS IN D. PSEUDOOBSCURA STORED FOR VARIOUS PERIODS OF TIME AT DIFFERENT TEMPERATURES

Storage time after feeding	Average number of cells per alimentary tract			
	Room temperature	15° C	5° C	0° C
Immediately after feeding	150,000	150,000	150,000	150,000
24 hours	65	300	3,200	93,000
48 hours	0	160	1,500	62,000

The flies were collected in a test tube which was cooled immediately by placing in a "super-ice" package. This is a commercial package consisting of an insulated box containing a frozen block[3] which holds the surrounding temperature at about 0°C. The container with flies was shipped on the evening of the collection enabling the isolation of yeasts from the flies early the next morning.

FATE OF YEAST CELLS IN THE DIGESTIVE TRACT OF DROSOPHILA

Although many investigators have shown the importance of yeast in the nutrition of Drosophila, there is no information indicating the effect of the digestive mechanism of Drosophila on yeast cells. In our work, the question arose as to whether or not fly pellets might be used as a source of cultures as indicated by the work of Hedrick and Burke (1950).

Flies (*Drosophila pseudoobscura*) were permitted to feed on bakers' yeast as indicated above. Fecal pellets were then collected on slides for examination. The direct microscopic examination of fecal pellets showed that they were composed almost entirely of intact rather than broken yeast cells. There was no indication of cell wall breakage during the digestive process. Upon applying a solution of methylene blue (1:100,000) to fecal pellets, the

[3] This block is a commercial preparation consisting of a mixture of sawdust and certain chemicals enclosed in a coarse fiber paper covering. In using the block, it is first submerged in water, then frozen at −6°F or less. When placed in the insulated box, it remains cold for a much longer period than does ice.

yeast cells stained instantly, indicating that they were killed by passage through the digestive tracts. Furthermore, microscopic examination revealed that each pellet contained 20-30 yeast cells and that practically all the cells were more or less empty. There was no evidence to indicate that more than a stray yeast cell, if any at all, could survive passage through the intestinal tract of *D. pseudoobscura.*

According to Lamanna and Mallette (1950), yeast cells are gram positive because of the presence of ribonucleate. Therefore, if this substance is removed, the cells should become gram negative. This proved to be the case upon application of the gram stain to yeast cells in fecal pellets, indicating the removal of ribonucleate during passage of the yeast cells through the digestive tract.

ACKNOWLEDGEMENT

The authors are indebted to Professor M. A. Joslyn for his many helpful suggestions.

LITERATURE CITED

Baumberger, J. P., 1919, A nutritional study of insects, with special reference to microorganisms and their substrata. J. Exp. Zool., 28:1-81.

Chevais, S., 1942, Development de la taille de l'oeil chez la nutent Bar de *Drosophila melanogaster.* Bull. Biol. France et Belg., 76:142-158.

Chiang, H. C., and Hodson, A. C., 1950, An analytical study of population growth in *Drosophila melanogaster.* Ecol. Monographs, 20:173-206.

Delcourt, A., and Guyenot, E., 1910, De la possibilité d'étudier certain Dipteres en milieu definite. C. R. Acad. Sci. Paris, 151:255-257.

Dobzhansky, Th., 1943, Genetics of natural populations. IX. Temporal changes in the composition of populations of *Drosophila pseudoobscura.* Genetics, 28:162-186.

Gordon, C., and Sang, J. H., 1941, The relation between nutrition and exhibition of the gene Antennaless (*Drosophila melanogaster*). Proc. Roy. Soc. Ser. B. 130:151-184.

Guyenot, E., 1913, Etudes biologiques sur une mouche, *Drosophila ampelophila* Loew. C. R. Soc. Biol., 74:97-99, 178-180, 223-227, 270-272, 332-334, 389-391, 443-445.

Hedrick, L. R., and Burke, G. C., 1950, Yeasts from Hawaiian fruit flies; their identification and ability to produce riboflavin. J. Bact., 59:481-484.

Lamanna, C., and Mallette, M. F., 1950, The relation of the Gram stain to the cell wall and the ribonucleic acid content of the cell. J. Bact., 60:499-505.

Leach, J. G., 1940, Insect transmission of plant diseases. 615 pp. McGraw-Hill Book Co., New York.

Northrop, J. H., 1917a, The role of yeast in the nutrition of an insect (Drosophila). J. Biol. Chem., 30:181-187.

1917b, The effect of prolongation of the period of growth on the total duration of life. J. Biol. Chem., 32:123-126.

Robertson, F. W., and Sang, J. H., 1944, The ecological determinants of population growth in a Drosophila culture. Proc. Roy. Soc. Ser. B. 132:258-291.

Vol. LXXXV, No. 825 The American Naturalist November-December, 1951

SELECTIVE DIFFERENCES BETWEEN MALES AND FEMALES IN DROSOPHILA ROBUSTA

MAX LEVITAN

Virginia Polytechnic Institute, Blacksburg, Virginia

INTRODUCTION

Carson and Stalker (1948) discovered that females of *Drosophila robusta* Sturtevant collected in the late summer and autumn near St. Louis, Missouri, were almost always virgin or uninseminated. A similar phenomenon was noted in collections of this species at Englewood Cliffs, New Jersey (Levitan, 1951a). Chromosomal analysis of the diapausing females of this species thus yielded an estimate of the frequencies of the gene arrangements in adult females of the population ("adult female sample"), in addition to the adult male and egg samples available as in other species. This made possible a comparison of the frequencies of the gene arrangements in the two sexes. The data suggested significant differences between the sexes for several arrangements, but the results could not be checked by further fall collections in that locality. Collections of *D. robusta* were, however, resumed near Blacksburg, Virginia. In this population selective differences between male and female carriers of the same gene arrangements have also been observed.

MATERIALS AND METHODS

Collections were made in North Crumpacker Woods, about one mile from the campus of Virginia Polytechnic Institute, in Montgomery County, approximately 2,100 feet above sea level. The vegetation is of the oak-hickory association, including also abundant wild cherry, black locust, dogwood, black haw, poison ivy, and blackberry. The methods of collection and analysis were described in a previous paper (Levitan, 1951a). To increase the accuracy of the analysis of adult samples, the salivary gland chromosomes of eight larvae were studied in the offspring of each male or virgin female collected. Determination of the chromosomal constitutions of females inseminated in nature was possible only when the single offspring (larva) examined was homozygous for a chromosomal arm; this gave evidence of one arrangement of that arm carried by the collected fly.

RESULTS

Tables 1–3 show the results obtained in the spring and fall of 1950. The spring data are from two samples (April 24–May 13 and May 30–June 8) and the fall data from three samples (August 24–September 4, September 23–October 1, and October 23–November 8). Within each season the samples are not significantly heterogeneous. In the adult female samples, 24 of the

TABLE 1

FREQUENCIES (IN PER CENT) OF X-CHROMOSOME ARRANGEMENTS IN NORTH CRUMPACKER WOODS, BLACKSBURG, VIRGINIA, 1950

Sample	n	XL	XL-1	XL-2	n	XR	XR-2
A. Adult females							
Spring	48	43.8	56.2	0.0	61	24.6	75.4
Fall	251	45.4	45.8	8.8	252	20.2	79.8
B. Adult males							
Spring	70	28.6	64.3	7.1	70	18.6	81.4
Fall	152	44.1	42.1	13.8	152	21.0	79.0
C. Totals*							
Spring	206	36.4	56.8	6.8	206	25.2	74.8
Fall	411	45.0	44.3	10.7	411	20.7	79.3
Grand total	617	42.1	48.5	9.4	617	22.2	77.8

*Differences between these totals and the sum of the adult samples is accounted for by the inclusion of all the egg sample data in the totals.

chromosomes in the spring and 246 of the chromosomes in the fall for each arm are from analyses of virgin females.

The frequencies of the arrangements in the left arm of the X-chromosome and in the left arm of the second chromosome show highly significant differences between spring and fall in the total data. Data from the spring, 1951, collections indicate that the changes are probably cyclic (Levitan, 1951b). The situation is presumably analogous to that observed in *D. pseudoobscura* by Dobzhansky (1943, 1948) and in *D. funebris* by Dubinin and Tiniakov (1946). However, males and females are not equally responsible for these changes. Thus, the differences between the spring and fall adult male samples for the XL arrangements are highly significant (Chi-square of 9.565 for two degrees of freedom), whereas the differences are not significant for the corresponding adult females. The significant changes in

TABLE 2

FREQUENCIES (IN PER CENT) OF SECOND-CHROMOSOME ARRANGEMENTS IN NORTH CRUMPACKER WOODS, BLACKSBURG, VIRGINIA, 1950

Sample	n	2L	2L-1	2L-2	2L-3	n	2R	2R-1
A. Adult females								
Spring	38	23.7	23.7	5.3	47.4	66	100.0	0.0
Fall	247*	25.5	19.8	19.4	34.8	252	94.0	6.0
B. Adult males								
Spring	140	25.0	22.1	11.4	41.4	140	89.3	10.7
Fall	303	28.7	22.8	21.8	26.7	303	88.4	11.6
C. Totals†								
Spring	276	26.1	22.5	11.6	39.9	276	90.2	9.8
Fall	567*	27.5	21.5	20.6	30.2	567	90.7	9.3
Grand total	843*	27.0	21.8	17.7	33.3	843	90.5	9.5

*Include one instance of arrangement 2L-5 (unpublished data), not included in the calculations discussed in the text.

†See footnote to Table 1.

the males occurred in the frequencies of XL and XL-1. On the other hand, the changes in the rarer arrangement, XL-2, are barely significant in the females (P about .04 for one degree of freedom) but not at all in the males. Similarly, the changes in the left limb of the second chromosome are highly significant in the males but not in the females. In females, significant changes are recorded only in 2L-2, since the test for heterogeneity between spring female 2L-2 and fall female 2L-2 give chi-square equal to 4.607, for which P is between .02 and .05 for one degree of freedom. In the males the changes are highly significant for both 2L-2 ($\chi^2 = 6.800$ for 1 d.f.) and 2L-3 ($\chi^2 = 9.601$ for 1 d.f.). The participation of both sexes in the 2L-2

TABLE 3

FREQUENCIES (IN PER CENT) OF THIRD-CHROMOSOME, RIGHT ARM ARRANGEMENTS IN NORTH CRUMPACKER WOODS, BLACKSBURG, VIRGINIA, 1950

Sample	n	3R	3R-1
A. Adult females			
Spring	50	50.0	50.0
Fall	249	54.2	45.8
B. Adult males			
Spring	140	52.1	47.9
Fall	302	54.0	46.0
C. Totals*			
Spring	276	51.4	48.6
Fall	566	54.4	45.6
Grand total	842	53.4	46.6

*See footnote to Table 1.

changes accounts partly for the absence of a significant difference between the frequencies of this arrangement carried by the sexes in the fall; on the other hand, the considerable seasonal change in 2L-3 in males but not in females is reflected by the fact that the sexes do show some significant differences in the proportions of 2L-3 they carry ($\chi^2 = 4.480$, with P between .02 and .05 for 1 d.f.). In XL, males and females show their largest ostensible differences in spring, but these differences are not statistically significant. The frequency of XR among adult females appeared to fall, and XR-2 to rise, between spring and autumn with an opposite change in the males, but neither change proved to be statistically significant.

Males seem to carry more 2R-1 and less 2R than females in both seasons. This difference is fairly significant in the fall data ($\chi^2 = 5.380$, $.02 < P < .05$ for 1 d.f.) and highly significant in the smaller spring data ($\chi^2 = 7.637$ for 1 d.f.).

Though 3R tends to be more common, and 3R-1 less common, in the fall than in the spring in all samples, the arrangements of the arm show no significant sexual or seasonal differences. Similar constancy was observed for 2L and 2L-1. In New Jersey 2L showed the most significant sex differences (Levitan, 1951a).

SUMMARY

Drosophila robusta collected in a Southwest Virginia woods show seasonal changes in gene arrangement frequencies in several chromosomal arms. Most of these changes are significant in males but not in females. The gene arrangements of one arm show no seasonal changes but differ significantly in the two sexes. The data indicate that the selection pressures on carriers of these gene arrangements are probably not identical in males and females.

ACKNOWLEDGEMENTS

The author is grateful to Professor A. B. Massey, of the Botany Section of the Department of Biology, Virginia Polytechnic Institute, for aid in identifying the vegetation of Crumpacker Woods, and to the Rockefeller Foundation for assistance in procuring the necessary equipment.

LITERATURE CITED

Carson, H. L. and H. D. Stalker, 1948, Reproductive diapause in *Drosophila robusta* Sturtevant. Proc. Nat. Acad. Sci. 34: 124-129.

Dobzhansky, Th., 1943, Genetics of natural populations. IX. Temporal changes in the composition of populations of *Drosophila pseudoobscura.* Genetics 28: 162-186.

1948, Genetics of natural populations. XIV. Altitudinal and seasonal changes produced by natural selection in certain populations of *Drosophila pseudoobscura* and *Drosophila persimilis.* Genetics 33: 158-176.

Dubinin, N. P. and G. G. Tiniakov, 1945, Seasonal cycles and the concentration of inversions in populations of *Drosophila funebris.* Amer. Nat. 79: 570-572.

Levitan, M., 1951a, Experiments on chromosomal variability in *Drosophila robusta.* Genetics 36: 285-305.

1951b, Response of the chromosomal variability in *Drosophila robusta* to seasonal factors in a Southwest Virginia woods. Rec. Gen. Soc. Amer. 20: 109-110.

Vol. LXXXV, No. 825 The American Naturalist November-December, 1951

THE SCENT-PRODUCING ORGAN OF THE MALE MONARCH BUTTERFLY

SIBYL A. HAUSMAN

Department of Zoology, Connecticut College

Wherever the common milkweed grows in the east during the spring and summer months, we find, often in large numbers, the familiar orange and black milkweed butterfly, or Monarch. The entomologist, artist and color photographer have helped to make this one of the best known of the insects. Its interesting and amazing habits of migration have been recorded by writers and by the motion picture camera. One who has observed the emergence of the adult from the green, gold-studded chrysalis has had an experience never to be forgotten.

Although Monarch butterflies are figured in almost every book concerned with insect study, it is by rather careful examination of the butterflies themselves that the sexes are determined. The female may be distinguished by somewhat darker coloration due to rather wide bands of black scales along the wing veins. In the male, the veins are more narrowly margined with black, and there is present, on the upper surface of each hind wing, a small, black patch adhering closely, though not connected, to the second cubitus vein (fig. 1, above). Similar structures on the wings of male butterflies are quite common and constitute a universal type of scent-producing organ in these insects.

The scent organ of the Monarch butterfly is a slightly elevated black pouch about three millimeters in length and one and one half millimeters in width. The darkly colored scales which cover it are similar to those found in the dark areas of the wings (fig. 1, center). In freshly caught specimens these scales can be readily brushed off with a fine brush. For dried insects, on the other hand, scraping with a fine blade is necessary in order to remove the scales. Removal of the scales exposes a slightly rounded portion of the ectoderm, like a small pocket, somewhat darkened and covered with specialized cells and tiny pits. Breaking through the thin covering, the inner cavity of the sac can be studied. Here is a lining of tiny, black, overlapping scales. These can be examined by scraping the inner wall with a fine knife or flattened, sharp needle, and mounting them on a microscope slide. They are much smaller and more delicate than the surface scales and more heavily pigmented. These are the "scent scales," or "androconia." The latter is a term widely used by the entomologist, with the appropriate meaning "male dust." The inner wall of the sac itself is thin, yellowish, and with regularly arranged circular areas, so-called "scent cups." Each is covered with a thin cuticle bearing a minute central pore from which extends an extremely narrow, hair-like scale, similar to a seta. Fitted into such pores are the scale stalks or pedicels in contact

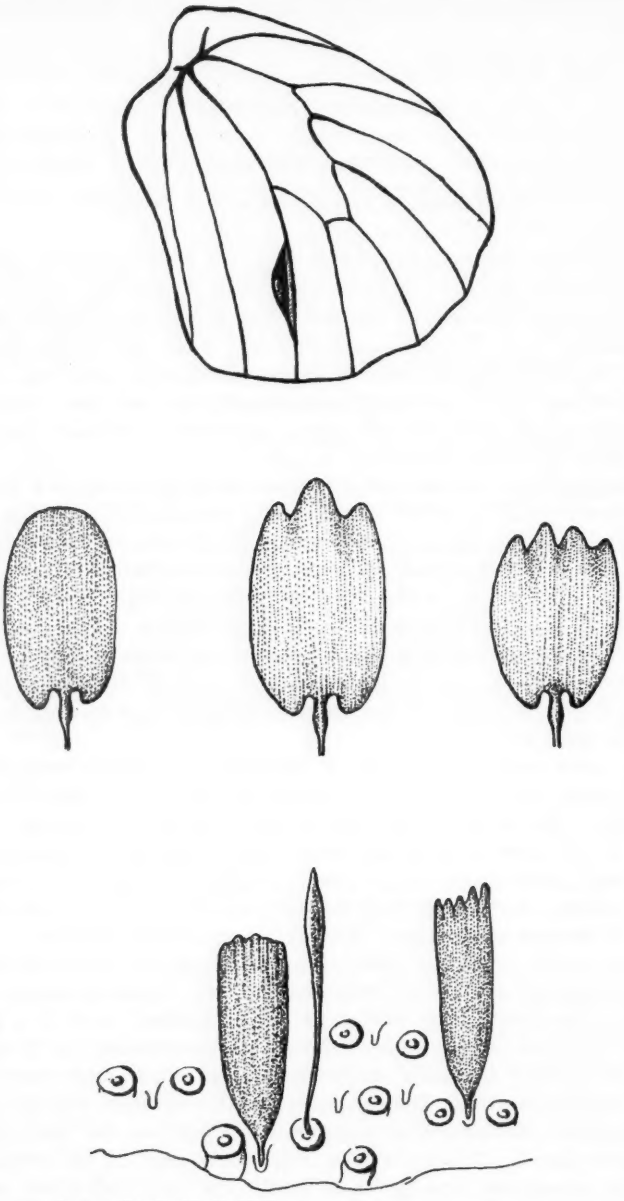


FIGURE 1. Above, hind wing of male showing scent organ; center, types of scales covering surface of scent organ; below, portion of inner wall of scent organ showing scent pits and scent scales.

with unicellular gland cells of the epidermis. In areas between the "cups" are pits in which are located the pedicels of wider scales (fig. 1, below). These two types of scales give off characteristic odors and would account for the term "scent scales" and for references to the sac as a "scent gland" or an area of "sensory scales." Secretions from specialized gland cells escape in the regions of the pedicels to coat the surfaces of the scales. Thus, these modified insect "hairs" serve as outlets for cell secretions. The secretory substance has a faint, fragrant odor likened to the sweet milkweed blossoms with which the insect is associated. It may serve, in function, as a sex stimulant in that it is attractive to the opposite sex. In freshly captured specimens, the fragrance can often be detected over and above the more pungent and unpleasant general body odor. The latter, being decidedly repulsive, is considered a protection against enemies.

It would seem, therefore, that the scent organ is capable of producing a very effective perfume. Recognized by the relatively "poor" sense organs of man, to the butterflies it probably serves as a powerful stimulant readily distinguishable to members of the species. Being peculiar to the males, it would be an aid in finding their mates.

Vol. LXXXV, No. 825 The American Naturalist November-December, 1951

BOOK REVIEWS

PALEONTOLOGY AND EVOLUTION

MARSTON BATES

The naturalist is interested in the diversity of living things: which means not only the description and analysis of the diversity of the present living world, but also the search for explanations. And this search for the explanation of living diversity, this preoccupation with organic evolution, provides the basic theme that binds all of natural history together and gives coherence to its superficially multifarious range of activities. Geneticists, paleontologists, ornithologists, taxonomists, mycologists, ecologists, morphologists, entomologists and so forth are all, after their distinctive fashions, attempting to throw light on the processes of evolution; even psychologists and physiologists, to the extent that they are studying the origin and diversification of their phenomena (the so-called "comparative" fields) are acting as naturalists. A new book on evolution must, then, be of interest to all of them.

And what a monumental book this is[1]: the summation of the thought and action of a long and fruitful life. Here Dr. Gregory has taken the essentials of his multitudinous observations and theories and fitted them neatly into the background of paleontological science, forming the whole into a unified scheme that can serve as a point of reference for what has been done, and as a point of departure for the observations of the future.

Essentially, this is a statement of the history of animals, especially of the vertebrates, as it is now known to us from the fossil record. It is, of course, illuminated by Dr. Gregory's extensive acquaintance with form and function in living animals; and the material is arranged so that from it there emerges a series of general principles—of anisomerism and polyisomerism, of divergence and convergence and progressive change. But it remains, still, an interpretation of history, an accumulation of observations and deductions based on an examination of the documents, the fossils.

A book like this stands in strong contrast to a book on evolution written by an experimental scientist, say a geneticist. Yet paleontology and genetics are equally sciences, and the methods of each are equally necessary to the development of an understanding of evolutionary processes. The contrast only serves to emphasize Conant's contention that it is folly to talk about "the scientific method": there are many sciences with many methods, all equally valid for their particular purposes; and the common denominator of science, whatever it may be, is surely not a method. The experimentalists sometimes seem to have got the upper hand, these days, in the pecking-

[1]Gregory, William King. Evolution emerging; a survey of changing patterns from primeval life to man. New York: The Macmillan Co., 1951. Vol. I, xxvi + 736 pp. (text); Vol. II, vii + 1013 pp. (illustrations). $20.00.

order among scientists; and the ultra-centrifuge boys tend to be a little condescending toward the fellows with butterfly nets and geological hammers. But the observational scientists can stand on their record; there is no reason to give way at the food trough.

Among the observational sciences, there is none with a more brilliant record than paleontology. Its accumulation of facts, deductions and generalizations is surely one of the great intellectual achievements of modern Western man, no less great because it is not susceptible to social perversion for the manufacture of bombs. It represents an extraordinary construction of interlocking concepts, based on the convergence of many lines of evidence, from bones and rocks and living organisms and patient examination of the action of physical forces. The paleontologists in our midst look like perfectly ordinary people, but they must represent some precious combination of genes and childhood influence that enables them to give the most painstaking attention to detail and yet keep their minds free for the most daring flights of imagination—flights that may be checked at any moment by some stubborn little fact, a molar tooth or fragment of a femur.

Yet paleontology, clearly, cannot tell us all about evolution. It gives us a frame into which our theories must fit, and provides us with ideas, with accounts of things that have happened and that must be explained in terms of processes that are now going on about us. The synthesis, the development of understanding of the total complex of processes, will perhaps become the function of some new sort of naturalist, who can combine the gleanings of the many special sciences: of the taxonomists, morphologists and comparative physiologists who have described the present diversity of living things; of the paleontologists who have accumulated the historical documentation; of the geneticists who have dissected the mechanisms of inheritance and variation; and of the ecologists who have formulated the principles of population dynamics and analyzed the operation of environmental forces. But before this new naturalist can begin to operate, each of us must formulate, synthesize and clarify the content of his special science, keeping in mind the needs and perspectives of this new, emerging field. This Dr. Gregory has done, providing us with a work that each of us can use in his special field, and that all of us can use in building toward this broader understanding of the living universe.

PUBLICATIONS RECEIVED

THE AMERICAN NATURALIST is glad to acknowledge here the receipt of books on biological and natural history subjects which are likely to be of interest to our readers. No undertaking to publish reviews is implied in this acknowledgment. Books for notice may be sent to:

EDITORIAL OFFICE
The American Naturalist
635 W. 247 St.
New York 71, N. Y.

Ahlgren, Gilbert H., Glenn C. Klinghan, and Dale E. Wolf, 1951. Principles of Weed Control. 368 p., ill. $5.50. John Wiley and Sons, Inc., New York, N. Y.

Barclay-Smith, Phyllis, 1951. A Book of Ducks. 34 p., 16 colored plates by Peter Sheapheard. Penguin Books Limited, Harmondsworth, Middlesex, England.

Beaufort, L. F. de, 1951. Zoogeography of the Land and Inland Waters. VIII, 208 p., 10 figs. $5.00. Sidgwick and Jackson, London, England. (Distributed in U.S.A. by The Macmillan Co.).

This gives rather sketchy descriptions of the major zoogeographical regions, largely in vertebrate terms, with frequent reference to the paleontological record.

Brown, A. W. A., 1951. Insect Control by Chemicals. 817 p. $12.50. John Wiley and Sons, Inc., New York, N. Y.

Hegner, Robert W., and Karl A. Stiles, 1951. College Zoology. 6th Ed. 911 p. $6.00. The Macmillan Company, New York, N. Y.

Hesse, Richard, 1951. Ecological Animal Geography. 2nd Ed. Rewritten and Revised by W. C. Allee and Karl P. Schmidt. 715 p. $9.50. John Wiley and Sons, Inc., New York, N. Y.

Higman, Harry W., and Earl J. Larrison, 1951. Union Bay, the Life of a City Marsh. VIII, 315 p., ill. $4.00. University of Washington Press, Seattle, Wash.

A delightful book—"nature writing" at its best. It is an account in clean, unpretentious prose of wild events in a city marsh. It is mostly concerned with birds, but there is a lot about man and other mammals. No scientist could quarrel with the descriptions of behavior and ecological relationships, yet the narrative will surely pick up and hold the interest of a casual reader with no biological background.

Huntington, Ellsworth, 1951. Principles of Human Geography. 6th Ed. Revised by E. B. Shaw. XVIII, 805 p., many maps, photographs and diagrams. $6.25. John Wiley and Sons, New York, N. Y.

Shaw's revision includes the insertion of many warnings that climate and topography do not explain all human institutions, but the strong flavor of environmental determinism remains with hardly any intrusion of the concepts of contemporary anthropology. The book might more appropriately be called "the physical background of human geography."

Imms, A. D., 1951. Insect Natural History. XVIII, 317 p., 40 colored plates; 32 plates in black-and-white; 40 text figures; 8 maps. $5.00. The Blakiston Company, Philadelphia, Pa.

A volume of the British *New Naturalist* series. The enormous erudition of the author is expressed in a prose that is always clear and often amusing; the photographs, both in color and black-and-white, are masterpieces; even the diagrams are models of precision and clarity. In short, there is no better book about insect life for the general reader. It is about British insects, but these hardly differ from their American relatives. The book should make a splendid text. The instructor could translate the examples into local terms and the student would be left owning a beautiful book of enduring value.

Lapage, Geoffrey, 1951. Parasitic Animals. XXI, 351 p., 113 figs. $4.00. Cambridge University Press, New York, N. Y.

A good review of the types of parasite life histories and of adaptations of parasite and host. The author has packed an amazing amount of information between the covers of his book, though with more emphasis on physiology than on ecology. The material is too detailed, and the writing too pedestrian, for popular appeal, and the scholar will be disappointed by the complete absence of documentation; the book should have a useful place, however, as an introduction to the phenomena of parasitism for the student of general biology.

Lawrence, George H. M., 1951. Taxonomy of Vascular Plants. 823 p., ill. $7.95. The Macmillan Company, New York, N. Y.

Lederberg, Joshua (Ed.), 1951. Papers in Microbial Genetics. 303 p. $3.75. University of Wisconsin Press, Madison, Wis.

Pettingill, Olin Sewall, Jr., 1951. A Guide to Bird Finding East of the Mississippi. 659 p., ill. $4.00. Oxford University Press, New York, N. Y.

Pitelka, Frank A., 1951. Speciation and Ecologic Distribution in American Jays of the Genus Aphelocoma. 269 p. and 13 plates. $3.00. University of California Publications in Zoology, Vol. 50, No. 3. University of California Press, Berkeley, Calif.

Prescott, G. W., 1951. Algae of the Western Great Lakes Area. 946 p., 136 plates. $10.50. Cranbrook Institute of Science, Bulletin No. 31. Bloomfield Hills, Mich.

Pyrenson, Louis, 1951. Elements of Plant Protection. 538 p., ill. $4.96. John Wiley and Sons, Inc., New York, N. Y.

Rosendahl, Carl Otto, and Frederic C. Butters, 1951. A Guide to the Spring

Flowers of Minnesota. 8th Ed. 108 p., ill. $2.25. Burgess Publishing Co., Minneapolis, Minn.

Sanderson, Ivan T., 1951. How to Know the American Mammals. 161 p., ill. 35 cents. The New American Library of World Literature, Inc. (Mentor Books), New York, N. Y.

Science Reports, Fourth Series, Vol. XIX, No. 1, 1951. 132 p. Biological Institute, Tohoku University, Sendai, Japan.

Shull, A. Franklin, 1951. Evolution. 322 p. $5.00. McGraw-Hill Book Company, Inc., New York, N. Y.

Simpson, George Gaylord, 1951. Horses. 247 p. and 32 plates. $6.50. Oxford University Press, New York, N. Y.

Smith, Lyman B., 1951. Studies in the Bromeliaceae, XVI. 92 p. Contributions from the U. S. National Herbarium, Vol. 29, Part 10. Smithsonian Institution, Washington, D. C.

Stanford, E. E., 1951. Man and the Living World. 2d Ed. 863 p. $5.50. The Macmillan Company, New York, N. Y.

Transactions of the Kansai Entomological Society, 1950. Vol. XV, Part 2, Nov., 1950. 68 p. Kansai Entomological Society, Nishinomiya, Hyogo-Ken, Japan.

Westveld, R. H., and Ralph H. Peck, 1951. Forestry in Farm Management. 2d Ed. 340 p., ill. $5.00. John Wiley and Sons, Inc., New York, N. Y.

Williams, Jay, 1951. Fall of the Sparrow. 158 p. $3.00. Oxford University Press, New York, N. Y.

"Fall of the Sparrow" is essentially an obit for the many species of animals and plants which have lived on this planet, but which are no longer with us. Some of them became extinct many ages ago; some only yesterday; some have been extirpated by man either inevitably through the destruction of the only habitat in which they could survive, or through man's greed or ignorance or curiosity. Sometimes the name of the murderer of the last individual and the date of the crime is known; sometimes the species has just vanished like the Cheshire cat's smile, after the number of its individuals had decreased to the point at which it could no longer recover from such disasters as droughts, epidemics, forest fires, or severe winters. Climatic changes have been responsible for the disappearance of many species, but man is the greater villain particularly in recent times. The sprightly manner of the writing, close-knit and economical of words, points up the gloomy nature of the story, which is alleviated, however, by a cheerful chapter toward the end of the book. This gives a short account of the controls which have been set up in many countries as well as internationally to prevent indiscriminate destruction, and of the ecological studies which may be expected to slow down, if not entirely to stop, the extinction of still more species in the future.

Woodruff, Lorande L., and George A. Baitsell, 1951. Foundations of Biology. 7th Ed. 719 p. $5.50. The Macmillan Company, New York, N. Y.

INDEX

NAMES OF CONTRIBUTORS ARE PRINTED IN CAPITAL LETTERS